UNIVERSITY OF ALBERTA

DYNAMICS OF THE BEAVER OF SASKATCHEWAN'S NORTHERN FOREST

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Dynamics of the beaver of Saskatchewan's northern forest", submitted by John Raymond Gunson in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Harvests and population dynamics of beaver were studied in 14 major habitats of Saskatchewan's northern forest between 1963 and 1968. Major habitats were distinguished on the basis of climatic, physiographic and vegetative differences.

The number of beaver harvested per square mile per year during the period 1958-59 to 1967-68 varied from 0.94 in Pasquia to 0.02 in Northern Transition. Differences in harvest were considered to be primarily a result of variations in habitat quality. Reduced harvests occurred in the mid 1960's and were related, at least in some areas, to population declines resulting from the high harvests of the late 1950's and early 1960's. Population increases in the Churchill and Hyper-Churchill habitats between 1965 and 1967 were related to restrictions on the harvest beginning in 1963-64. The trappers' census was judged an imprecise measure of population size over large areas. An alternative method of estimating population size was developed and recommended for further use.

Numbers of beaver in colonies varied significantly between the two habitats intensively studied suggesting that colonies in higher quality habitats contained more beaver. The number of beaver in colonies appeared to be regulated by variations in litter size and in the frequency of dispersal of immature animals.

Studies of beaver in an intensive study area of inferior habitat indicated high survival of kit beaver in the first few months of life, movements of entire family-groups into and out of the study area, and emigration of yearlings from parental colonies in their second summer of life.

Growth rates and reproductive performance were highest in high

quality habitats containing greater proportions of the preferred food species, the poplars. Ovulation rates varied from 5.20 ± 0.61 in the fringe area immediately south of the trapline areas to 3.00 ± 0.63 in the Uranium City habitat. Calculated losses from resorption varied between 1.8 percent in South-Saskatchewan to 13.8 percent in Uranium City.

Litter size of beaver varied directly with availability and presumably quality of preferred foods and with body weight, and perhaps inversely with population density. Temperature variations and latitude appeared to have no effect on litter size. Litter size of Porcupine beaver increased from 3.50 ± 1.09 for yearlings to 4.85 ± 1.23 for 8-year olds and then declined with increasing age.

Pregnancy rates of adults were over 85 percent in all habitats but Uranium City, where the rate was 71.4 percent. Yearlings, 2-year olds and beaver over 12 years of age bred less frequently than adults from 4 to 12 years of age.

Sex ratios were balanced at birth and, in harvest, favoured males slightly in the first year of life and females in the adult age-groups except the very old where males again predominated. A selection for adult females in the harvest was suggested.

Productivity varied between habitats with kits representing 51.5 percent in Pasquia and 23.4 percent in Foster. Mortality rates were highest in the first 2 or 3 years of life and lowest between the ages of 5 and 9 years. Differences in age-specific mortality rates were judged to be a result of mortality agents other than trapping. Mortality was much more rapid in the southern high quality habitats and this appeared to be a result of the more intensive trapping in such areas as indicated by tag recovery rates. Predation was considered an important mortality agent especially in more northern habitats.

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TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION.. 1

DESCRIPTION OF STUDY AREAS.................................... 4

Climate... 4

Physiography.. 4

Vegetation.. 5

Beaver Habitats... 7

Pasquia and Porcupine... 8

Bronson and Meadow Hills...................................... 9

Mostoos Upland.. 9

Prince Albert Uplands... 10

Cub... 10

Hyper-Churchill and Manitoba Lowland.......................... 11

Churchill... 11

Foster.. 12

Athabasca... 12

Uranium City.. 12

Northern Transition... 13

South-Saskatchewan.. 13

METHODS... 14

Determination of Harvest...................................... 14

Determination of Population Trends............................ 14

Determination of the Accuracy of the Trappers' Censuses....... 15

Page

Determination of Colony Composition........................ 16

Determination of the Dynamics of the Cub Beaver............. 17

Determination of Growth Rates.............................. 19

Measurements of Reproductive Performance.................... 19

Field Collections...................................... 19

Ovary Examination...................................... 20

Counts of Fetuses and Resorptions...................... 21

Sex Determination.. 21

Age Determination.. 22

Determination of Trapping Intensity........................ 23

Statistical Analysis....................................... 23

RESULTS.. 25

Harvests and Population Changes............................ 25

The Harvest: 1946 to 1967-68........................... 25

Population Changes: 1946 to 1963-64.................... 25

Accuracy of the Trappers' Census: 1964 to 1967......... 28

Population Changes: 1963-64 to 1967-68................. 28

Factors Influencing Harvests and Population Changes:

1946 to 1963-64.................................... 32

Factors Influencing Harvests and Population Changes:

The Study Period................................... 34

Relationship of Harvest and Population Change.......... 34

Harvest Per Square Mile: A Rating of Habitats.......... 35

Colony Composition... 35

Colony Types... 35

Family-group Colonies.................................. 36

Page

Pair Colonies.................................... 36

Single-occupant Colonies.......................... 40

Beaver of the Intensive Study Area.................... 40

Number of Beaver in Colonies...................... 41

Movements of Beaver............................... 41

Emigration of Immature Animals from Parental Colonies. 44

Survival And Loss of Young Beaver in the Intensive Study Area.................................. 45

Years of No Reproduction.......................... 46

Kill-trapping and Colony Composition.............. 46

Harvest Following the Fourth Summer of Colony Occupation................................. 47

Some Spring Observations at Colony 2-63............ 47

Growth.. 48

Reproduction.. 48

Ovulation Rates................................... 48

Fetal Rates....................................... 51

Prenatal Mortality and Resorption Rates............. 51

Pregnancy Rates................................... 55

Variations in Reproductive Performance Between Years.. 55

Relationship of Environmental Factors to Reproductive Performance....................................... 57

Latitude and Reproductive Performance.............. 57

Winter Diet and Reproductive Performance............. 57

Climate and Reproductive Performance................. 59

Population Density and Reproductive Performance....... 61

Page

Age and Reproductive Performance........................ 63

Body Weight and Reproductive Performance................. 66

Minimum Breeding Age.. 66

Periods of Conception and Birth............................. 68

Sex Ratios.. 68

Age Structures.. 72

Variations of Age Structure Between Habitats............. 72

Variations of Age Structure Between Years................ 76

Survival and Mortality................................... 76

Observations of Mortality from Causes Other Than Trapping...... 79

Trapping Intensity.. 80

DISCUSSION.. 82

The Effect of Harvest on Population Changes................. 82

The Regulation of Beaver Numbers in Colonies................ 83

Habitat Quality and Types of Colonies....................... 84

The Regulation of Reproduction.............................. 85

The Breeding of Yearling Beaver............................. 89

Productivity.. 91

The Sources of Mortality.................................... 93

Trapping... 93

Predation.. 94

Disease.. 95

Others... 96

Variations in Survival and Mortality........................ 96

Habitat and Mortality.................................... 97

Age-specific Mortality................................... 98

Page

Sex-specific Mortality.................................. 98

Beaver and Trapping in Low Quality Habitats..................101

CONCLUDING DISCUSSION AND RECOMMENDATIONS........................103

LITERATURE CITED...106

APPENDIX I. Mean winter temperature (°F) and precipitation levels (inches) at recording stations in or near major beaver habitats...........................114

II. Ovulation rates of Saskatchewan beaver................115

III. Fetal rates of Saskatchewan beaver...................116

IV. Pregnancy rates of adult Saskatchewan beaver..........117

V. Prenatal mortality of Saskatchewan beaver.............118

VI. Resorption rates of Saskatchewan beaver...............119

VII. Frequency of beaver of various ages in the 1965-66 harvest in Saskatchewan..............................120

VIII. Frequency of beaver of various ages in the 1966-67 harvest in Saskatchewan..............................121

IX. Frequency of beaver of various ages in the 1967-68 harvest in Saskatchewan..............................122

LIST OF TABLES

Page

Table 1. Harvests of beaver in Saskatchewan habitats between 1958-59 and 1967-68.................................... 27

Table 2. Saskatchewan trappers' beaver census compared with ground, aerial and plot surveys: 1964 to 1967......... 29

Table 3. Number of beaver colonies per square mile of Saskatchewan habitat................................... 33

Table 4. Proportions of colonies with one, two and more than two beaver trapped in various habitats................ 37

Table 5. Mean numbers of beaver trapped per colony in two habitats.. 38

Table 6. Ages of beaver in a) adult pairs of family-group colonies, b) pair colonies and c) single-occupant colonies.. 39

Table 7. P values indicating the significance of the differences between means of fetal rates of Saskatchewan beaver.................................... 53

Table 8. Pregnancy rates (%) of beaver in the South-Saskatchewan and 11 NFCA habitats.................... 56

Table 9. Fetal rates of the beaver in various areas of its North American range: arranged in increasing latitude.. 58

Table 10. Climatic records and reproductive performance of beaver in four habitats........................... 60

Page

Table 11. Beaver density and fetal rate.......................... 62

Table 12. Colony size and fetal rate............................. 62

Table 13. Comparisons of actual female breeder proportions to potential breeder proportions in various habitats.... 65

Table 14. Body weights and fetal rates of Cub beaver............. 67

Table 15. Fetal, summer and winter sex ratios of Saskatchewan beaver (% males)....................................... 70

Table 16. Order of capture of kill-trapped beaver in 21 family-group colonies in the intensive study area and the Peter Burym trapline........................... 73

Table 17. Cumulative mortality rates of beaver in eight NFCA habitats.. 78

Table 18. Tag recovery rates of beaver in four NFCA habitats...... 81

Table 19. Sex ratios of beaver in trappers' harvests (% males).... 99

LIST OF FIGURES

		Page
Figure 1.	Conservation Areas in Saskatchewan's northern forest	2
Figure 2.	Map of Saskatchewan with beaver habitats and Rowe's forest classification	6
Figure 3.	The intensive study area in the Cub habitat showing locations of beaver colonies live-trapped and/or kill-trapped between 1964 and 1967	18
Figure 4.	Harvests of beaver in Saskatchewan: 1946-47 to 1967-68	26
Figure 5.	Trends in population size from the trappers' census	30
Figure 6.	Beaver at specific colonies in the intensive study area between 1964 and 1966-67	42
Figure 7.	Body weights of beaver by age in the Porcupine and Cub habitats: sexes combined	49
Figure 8.	Ovulation rates of beaver in 11 NFCA habitats and the South-Saskatchewan	50
Figure 9.	Fetal rates of beaver in 11 NFCA habitats and the South-Saskatchewan	52
Figure 10.	Prenatal mortality and resorption rates of beaver in 11 NFCA habitats and the South-Saskatchewan	54

Page

Figure 11. Age-specific fetal rates of the Porcupine beaver: 1965 to 1968 data combined.......................... 64

Figure 12. Scatter diagram of mean fetal lengths from eight habitats in 1968.................................... 69

Figure 13. Age structures of the beaver harvest in eight NFCA habitats: 1965-66, 1966-67 and 1967-68 harvests combined................................. 74

Figure 14. Survivorship curves of the Pasquia and Cub populations: 1965-66 to 1967-68 age data combined... 77

INTRODUCTION

In the introduction of his classic book, "The Fur Trade in Canada", Harold Innis (1930:3) wrote:

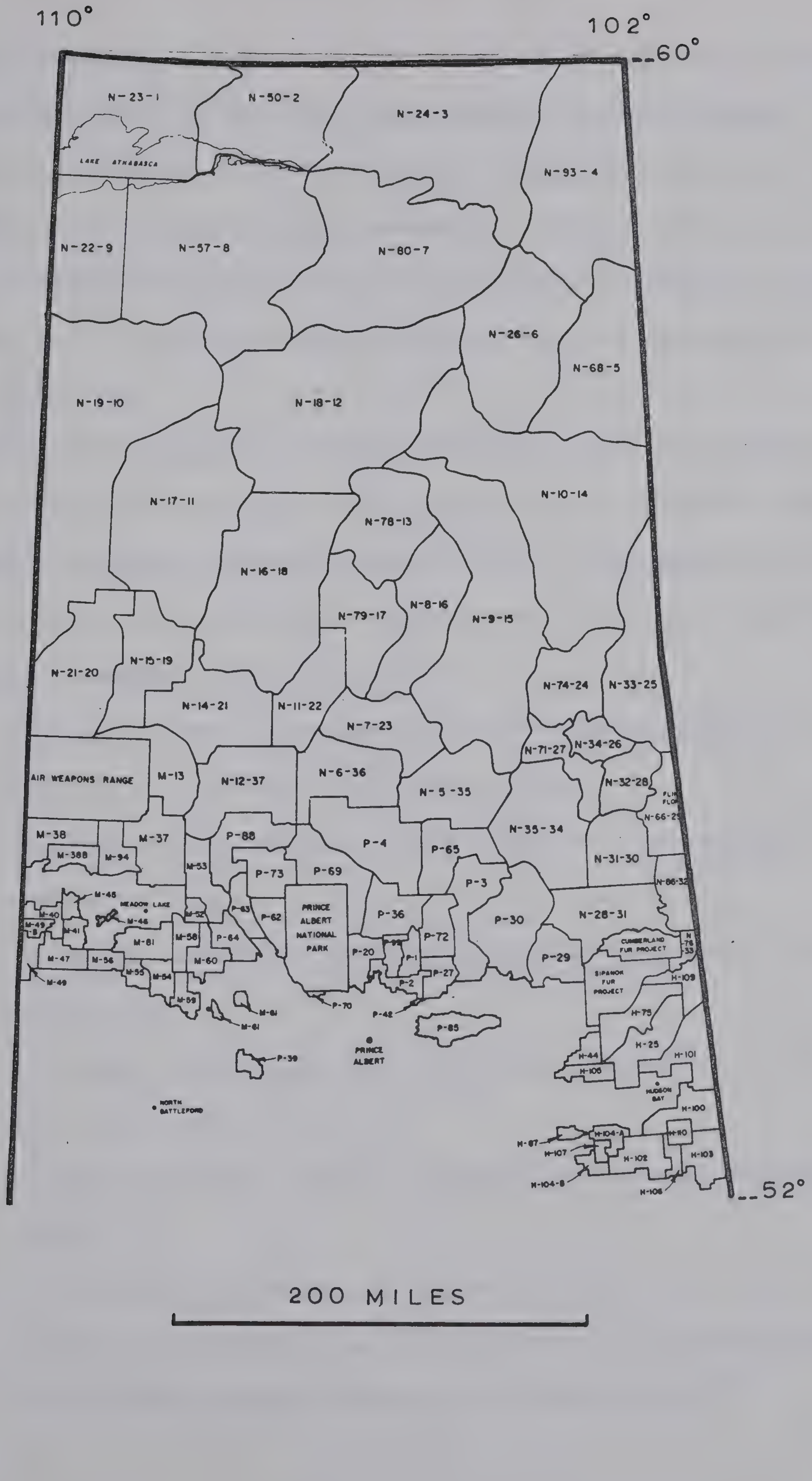
> "The history of Canada has been profoundly influenced by the habits of an animal which very fittingly occupies a prominent place on her coat of arms."

The beaver *Castor canadensis* Kuhl has long been Saskatchewan's most important fur-bearing animal, and has been especially important in the northern two-thirds of the province where harvests of thousands of animals annually have been vital in maintaining and developing the economy. Most trappers in the northern forest spend much of their trapping time in the "beaver hunt". Consequently much of their yearly earnings from fur trapping result from sales of beaver pelts.

The Northern Fur Conservation Area (NFCA) program, begun in 1946 as a joint federal-provincial project, provided funds for the development and more intensive management of northern Saskatchewan fur resources. Traplines were grouped into Conservation Areas (Fig. 1). Trappers from each Area held annual meetings to discuss fur management, reported their beaver census and set their beaver harvest limits or quotas. Government-trapper co-operation, centered on the beaver census, formed the core of the beaver management program that continues to this day.

Prior to 1946 less effective laws allowed widespread over-trapping of much of Saskatchewan's beaver population. During the first half of the 1900's many northern people never saw a beaver. One of the first major projects following the establishment of the NFCA was the transplantation of beaver from southern locations to various areas of the northern forest. Between 1946 and 1952 over 3,000 beaver were moved north. Low

Figure 1. Conservation Areas in Saskatchewan's northern forest. Each Area is a grouping of traplines.



110°
102°
60°
52°
N-23-1
N-50-2
N-24-3
LAKE ATHABASCA
N-93-4
N-22-9
N-57-8
N-80-7
N-26-6
N-68-5
N-19-10
N-18-12
N-10-14
N-17-11
N-78-13
N-16-18
N-8-16
N-79-17
N-9-15
N-21-20
N-15-19
N-14-21
N-11-22
N-74-24
N-33-25
N-7-23
N-71-27
N-34-26
AIR WEAPONS RANGE
M-13
N-12-37
N-6-36
N-5-35
N-32-28
N-66-29
M-38
M-37
P-88
P-4
P-65
N-35-34
M-388
M-94
N-31-30
M-53
P-73
P-69
P-3
N-86-32
M-45
MEADOW LAKE
PRINCE ALBERT NATIONAL PARK
M-46
M-52
P-63
P-62
P-36
P-30
N-28-31
M-40
M-41
M-81
M-58
P-64
P-72
CUMBERLAND FUR PROJECT
M-47
M-56
M-60
P-20
P-1
P-29
M-55
M-54
P-2
P-27
SIPANOK FUR PROJECT
H-109
M-49
M-59
P-70
P-42
H-75
M-61
P-85
H-25
H-101
PRINCE ALBERT
H-44
H-106
P-39
HUDSON BAY
NORTH BATTLEFORD
H-100
H-104-A
H-110
H-87
H-107
H-102
H-103
H-104-B
H-108
200 MILES

harvest limits were rigidly enforced during the early years of the program.

Following inauguration of the NFCA program harvests rose sharply until over 50,000 pelts were being sold annually in the province. This ideal situation was short-lived. Harvests were again declining by the mid 1960's. The reasons for such changes in abundance were poorly understood and pointed out the need for research and more intensive management. In 1963 I initiated studies of the ecology and management of beaver in the NFCA.

Studies were planned to provide information about the population dynamics of beaver from subunits or "habitats" of its northern Saskatchewan range. Long-term objectives were to relate differences in dynamics, if any, to differences in habitat conditions or variations in trapping intensities. Immediate objectives were:

1. To evaluate the relationships of harvest and population changes since 1946, and during the years of study.
2. To evaluate the trappers' beaver census as a measurement of population size.
3. To develop alternative methods of estimating population size, if necessary.
4. To compare the numbers, sexes and ages of beaver in colonies in various habitats.
5. To investigate the ecology of beaver in an area of inferior habitat.
6. To compare growth rates, reproduction, sex and age proportions, and mortality rates of beaver in habitats of different quality.
7. To determine trapping intensities in some habitats.

DESCRIPTION OF STUDY AREAS

The province of Saskatchewan is located near the center of the continental land mass of North America. The northern forest extends from about latitude 52°, the southern edge of the Porcupine Hills, to latitude 60°, the Northwest Territories border. Information on weather was supplied by the metereological station of the federal Department of Transport in Prince Albert. The Saskatchewan Institute of Pedology provided physiographic descriptions of some areas. Vegetative characteristics have been taken from Rowe (1959) and from my personal knowledge of the areas.

Climate

The climate of the area is greatly influenced by the Cordillera of western Canada and the relatively northern location. The Cordillera intercepts the prevailing warm, moist, westerly winds resulting in reduced precipitation, and allows entrenchment of cold arctic air masses in winter. Temperatures are below freezing for long periods during winter months. The frost-free period generally extends from about mid-May to September 1 in the southern forest areas and is less than three months in the northern areas. Summers are short and hot. Mean winter temperatures and levels of rain and snowfall from 1964-65 to 1967-68 are shown in Appendix I.

Physiography

The physiographic features of the area as expressed by relief,

drainage and local topography are varied and complex. The area includes portions of the Churchill Province of the Canadian Shield and of the Central Lowlands, Great Plains and Northern Plains Provinces of the Interior Plains Division of North America (Clayton 1960). The Canadian Shield occupies over half of the area and is characterized by exposed igneous and metamorphic rocks of Precambrian age scoured by glaciers, sand deposits and poor soil development of either weak podzols or peats. Immediately south of the shield are lowland areas extending across the province in the location once occupied by glacial lakes Hyper-Churchill and Agassiz. Lowland features of imperfect drainage and muskeg soil development, and sand deposits are common.

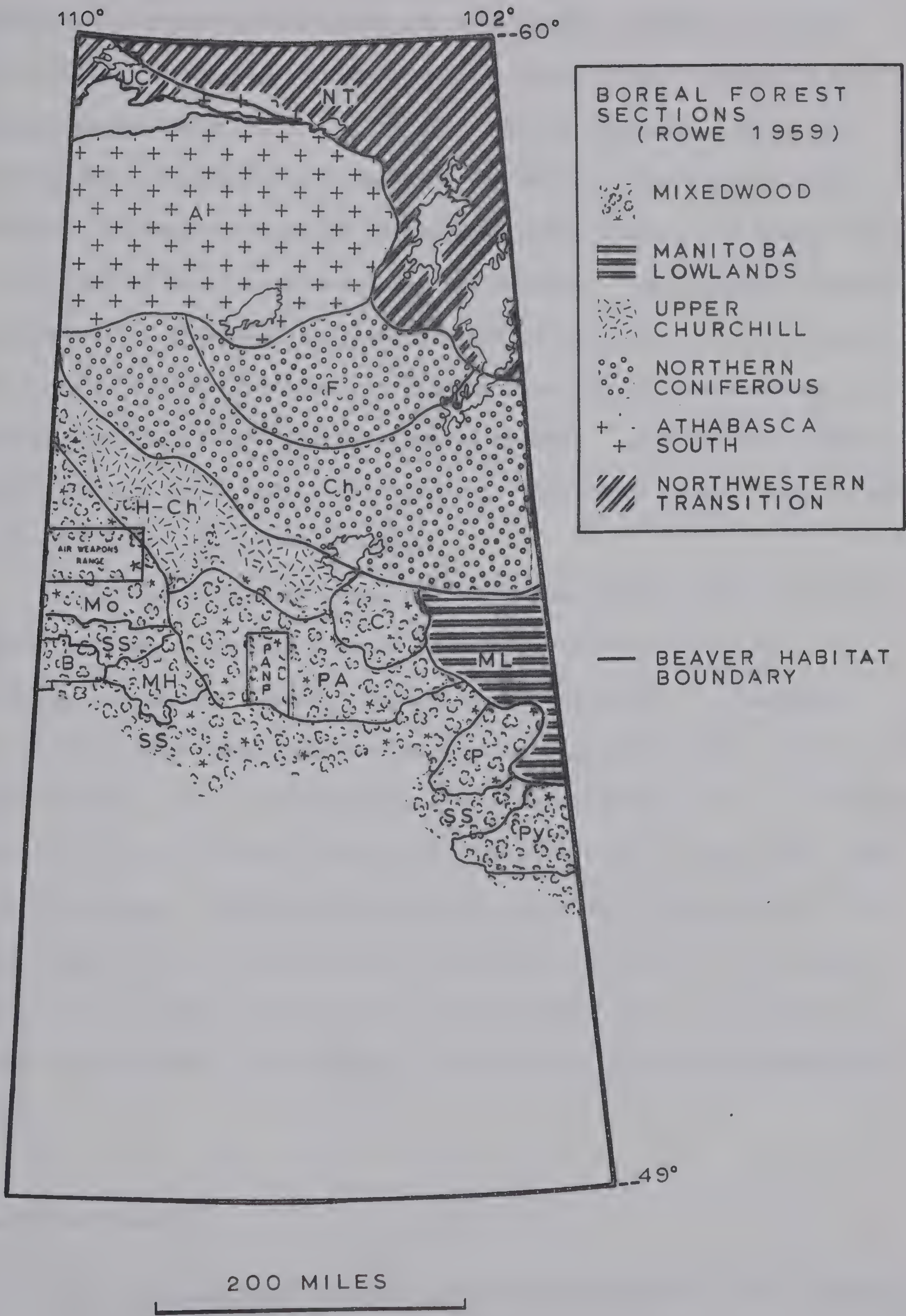
Farther south are a series of thinly-glaciated upland areas, the Porcupine, Pasquia, Cub-Wapawekka, Prince Albert and Mostoos hills. Soils of these hill areas are mainly grey wooded podzols with sandy deposits and some organic peats in poorly-drained areas. Two areas of glacial outwash origin, Bronson and Meadow Hills, are located on the southwestern extremity of the northern forest. Soils in the latter hills are primarily of grey wooded type. Elevations range from 600 feet in Athabasca to about 2,500 feet in most of the southern uplands.

Vegetation

All northern Saskatchewan forests are within the Boreal Region (Rowe 1959). In Saskatchewan parts of six sections of this region occur (Fig. 2). The Mixedwood Section includes all the upland habitats and the Bronson and Meadow Hills areas. This section is characterized by varying proportions of aspen *Populus tremuloides*, balsam poplar *Populus*

Figure 2. Map of Saskatchewan with beaver habitats and Rowe's (1959) forest classification. The South-Saskatchewan (SS) includes that portion of the Mixedwood Section south of the beaver habitats.

P	Pasquia
Py	Porcupine
B	Bronson
MH	Meadow Hills
PA	Prince Albert Uplands
ML	Manitoba Lowland
Mo	Mostoos
H-Ch	Hyper-Churchill
Ch	Churchill
C	Cub
F	Foster
A	Athabasca
UC	Uranium City
NT	Northern Transition
PANP	Prince Albert National Park


110°
102°
60°
49°
BOREAL FOREST SECTIONS (ROWE 1959)
MIXEDWOOD
MANITOBA LOWLANDS
UPPER CHURCHILL
NORTHERN CONIFEROUS
ATHABASCA SOUTH
NORTHWESTERN TRANSITION
BEAVER HABITAT BOUNDARY
AIR WEAPONS RANGE
P A N P
NT
UC
A
F
Ch
H-Ch
Mo
SS
B
MH
PA
C
ML
P
Py
200 MILES

balsamifera, white birch *Betula papyrifera*, white spruce *Picea glauca* and balsam fir *Abies balsamea* on the well-drained uplands; jackpine *Pinus banksiana* on sandy areas; and black spruce *Picea mariana* in poorly-drained parts including the basin-like tops of the hills. Rowe calls the lowland area immediately south of the shield, the Upper-Churchill Section. Extensive stands of jackpine on sandy plains, and black spruce on intervening poorly-drained areas predominate. The Coniferous Section, containing the Churchill and Foster habitats has closed forests wherever depth of soils is adequate. Black spruce is the dominant tree on poorly-drained lowlands and thin-soiled uplands. Jackpine and tamarack *Larix laricina* occur extensively as well. Scattered aspen, balsam poplar, white birch and white spruce occur.

Farther north the Athabasca South Section, which contains the Athabasca habitat, comprises a broad lowland of jackpine on sandy soils. Black spruce is also common. Poplars and white spruce are uncommon. The Northwestern Transition Section of Rowe's classification occupies the most northerly area in Saskatchewan, that represented by the two habitats, Uranium City and Northern Transition. This section is one of open, subarctic woodland. Unfavourable climatic conditions, thin soils and frequent fires reduce the distribution, abundance and size of tree species. Areas of bog, muskeg and bare rock are intermixed with open stands of dwarfed black spruce and jackpine. Some stunted aspen and balsam poplar occur.

Beaver Habitats

I made a preliminary division of the northern forest into 14 habitats

on the basis of climate, physiography and vegetation (Fig. 2). The subdivisions south of the Canadian Shield were adopted, in part, from Kirby's (1962) forest classification. In future, when more intensive management is possible, these large habitats may be subdivided into smaller units. This tentative classification may also have some use in studies of other game and fur species in northern Saskatchewan.

Pasquia (P) and Porcupine (Py)

The above two habitats, which rise between 1,500 and 2,000 feet above the surrounding countryside, are located, respectively, north and south of the village of Hudson Bay. The escarpment portions of both the Pasquia and Porcupine have fertile clay and clay-loam soils developed from lacustrine action in post-Lake Agassiz times. The P^H of these soils approaches neutrality. Some very fertile dark grey wooded soils occur in the southern parts of Pasquia. Both areas have numerous small lakes and streams that drain to the lowlands surrounding the hills. Precipitation is high and water levels are more easily maintained than in other habitats of the fringe region. Logging operations have reduced much of the forests to the second-growth stage. Aspen is the major tree species of both habitats and is readily available to beaver. The basin-like tops of the hills, especially in Pasquia, support some softwood vegetation. Beaver are especially abundant in the broad escarpments of these uplands.

Pasquia includes Conservation Areas H-25, H-44, H-75, H-105 and the westerly extensions of H-101 and H-109. It is approximately 2,600 square miles in area. Porcupine, 2,700 square miles, includes H-100, H-102,

H-103, H-104A, H-104B, H-106, H-107 and H-110.

Bronson (B) and Meadow Hills (MH)

The topography of these two habitats, located southwest and south of the town of Meadow Lake, is gently rolling. Areas of muskeg and mixtures of grey wooded sandy loams and sands occur. The Bronson forest has more irregular topography, sands and peaty meadows, and a history of repeated forest fires. The fires have created almost exclusive second-growth vegetation consisting of aspen, white spruce and jackpine. The high availability of aspen favours beaver in Bronson. Logging operations in Meadow Hills continue to reduce the mature segment, although some mature forest still remains.

Precipitation is lower in this area than in the eastern parts of the province (Appendix I). As a result water levels are not as well maintained, and in dry years beaver are hard pressed to secure sufficient water in ponds. This is partially attributable to the poor water holding capacity of the sandy soils. Some large lakes in the area act as reservoirs and help to maintain beaver populations. Areas of Bronson and Meadow Hills are 1,200 and 1,800 square miles, respectively. The Bronson habitat includes Conservation Areas M-40, M-41, M-45, M-47, M-49, M-49B and M-56. Areas included in Meadow Hills are M-52, M-54, M-55, M-58, M-60 and M-81.

Mostoos Upland (Mo)

This habitat has some very irregular topography, with altitudes reaching up to 2,500 feet, mainly grey wooded soils and some large areas

of muskeg. Hardwoods, aspen and birch are readily available to beaver along numerous streams and lakes. Water levels are maintained somewhat better than in areas immediately south. Conservation Areas included are M-37, M-38, M-38B, M-94 and N-21. A large section of the habitat is not available for trapping as it is used as an air weapons range by the Air Division of the Canadian Forces. This reduced the trapped portion to about 4,000 square miles.

Prince Albert Uplands (PA)

Grey wooded soils of primarily sandy loam texture, large areas of sand plains and huge muskegs are found in this habitat, a combination of a number of uplands. Forests with aspen as the major tree species occur sparingly. Jackpine on sands, and black spruce in muskegs and upland areas are common. In the southern parts of this habitat of 7,900 square miles, water levels drop to extremely low levels in dry years. Beaver have to hunt for supplies of aspen or locate in willow *Salix* areas in creek bottoms. Conservation Areas included are P-1, P-2, the southern section of P-3, P-20, P-27, P-62, P-63, P-64, P-69, P-72, P-73, P-88, P-99 and M-53. Prince Albert National Park is located in this habitat. Beaver were not trapped in the Park during the study period.

Cub (C)

Sandy outcroppings and muskegs are common in this habitat of 3,100 square miles which rises some 1,500 feet above the lowlands. Water levels are reasonably well maintained, probably chiefly because of increased precipitation in these uplands over that of surrounding areas. Large

areas of mature black spruce forest and some areas of fire-created jackpine regeneration have limited value for beaver. Willow, alder *Alnus rugosa*, white birch and jackpine contribute substantially to the diet of the beaver. Included in this habitat are P-65, the northern section of P-3, the Wapawekka Hills of N-5, and a small western part of N-35. The intensive study area is located in the Cub habitat.

Hyper-Churchill (H-Ch) and Manitoba Lowland (ML)

These two large lowland areas with elevations between 850 and 1,200 feet and situated immediately south of the shield area, are characterized by poor drainage, muskeg or sandy soils, a predominance of conifer vegetation, and little aspen. The Hyper-Churchill, 10,200 square miles in area, includes the western part of N-5, N-6, N-12, N-14, N-15, the southern part of N-19, M-13 and P-4. Areas included in Manitoba Lowland are H-101, H-109, N-28, N-31, N-86 and most of each of N-35, P-29 and P-30. This latter habitat is about 6,300 square miles in area.

Churchill (Ch)

Churchill, the largest of the beaver habitats, incorporating some 27,400 square miles of the Canadian Shield of from 950 to 1,760 feet in elevation, encompasses the watersheds of the Churchill and Reindeer Rivers. Lakes, rivers and other water bodies are abundant and deep. The area was subjected to intense glaciation. Consequently soils are acidic, thin over rock and peaty in depressions. Some sand deposits occur and bedrock outcroppings are common. Conifer forests predominate, but some areas of second-growth with hardwoods exist that result from

periodic fires. In river valleys, around some of the lakes and on south-facing slopes, where more favourable conditions of soil and local climate exist, white spruce, balsam fir, aspen and balsam poplar form mixed stands of good growth. The following areas are included: N-7, most of each of N-8, N-9, N-11 and N-79 as well as N-16, N-17, N-32, N-33, N-34, N-71, N-74 and the southern half of N-10.

Foster (F)

I have tentatively divided Rowe's Coniferous Section into two habitats. The Foster is the more northerly portion. It differs from the Churchill in having a greater proportion of mature forest, mainly black spruce. Some areas of fire-created second-growth occur that include jackpine, birch and aspen. The habitat includes N-26, N-78 as well as the northern portions of N-8, N-9, N-10, N-11 and N-79; and is approximately 11,100 square miles in size.

Athabasca (A)

The large habitat of Athabasca, about 26,700 square miles with elevations between 600 and 1600 feet, consists of a broad lowland of sand plains supporting stunted jackpine, and poorly drained lowlands of black spruce. Lakes are either muskegy or sandy-shored. Hardwoods are not common and beaver are scarce. Areas included are N-18, N-22, N-57, N-80 and the northern half of N-19.

Uranium City (UC)

Although Rowe included this small area of 1,700 square miles in the

Northwestern Transition Section, I feel that significant variations from the forests of that section exist. The topography along the north shore of Lake Athabasca is extremely irregular. As a result water bodies are abundant and deep. In addition, the growth of aspen is favoured along the numerous southern-exposed hills. Consequently beaver are well-established and populations were high during the study period. Most of N-23 and a narrow strip north of Lake Athabasca in N-50 are included.

Northern Transition (NT)

A scarcity of hardwoods and long, cold winters render this area unsuitable for beaver. Populations are thinly scattered. The habitat of 22,600 square miles includes N-24, N-50, N-68, N-93 and the north-eastern portion of N-23.

South-Saskatchewan (SS)

The South-Saskatchewan includes that portion of Rowe's Mixedwood Section south of the beaver habitats (Fig. 2). This area is settled and farmed. There is a complex mixture of soils present, but generally the soils are more productive than those of the forested areas (Moss 1965). The poplars are very common throughout this region.

METHODS

Determination of Harvest

Numbers of beaver trapped and sold annually from each Conservation Area are calculated and published by the Statistics Division of the Saskatchewan Wildlife Branch. The raw data for these calculations are taken from fur-dealer returns which list numbers of beaver sold by each trapper. Harvest records for both the NFCA and the area of the province south of the traplines are complete for the seasons 1946-47 to 1967-68. Adjustments were made where habitat boundaries did not fit Conservation Area limits. In such cases proportions of the harvest taken in each habitat were estimated. A more complete method would have been to use individual trapline harvests, but these were not available for all Areas and years.

Harvest per square mile of habitat was determined by dividing the mean of the yearly harvests for the 10 year period by the area. Area in square miles was calculated using a grid of squares on small scale maps.

Determination of Population Trends

Population trends were determined by utilizing the trappers' census and densities of beaver colonies on sample plots.

The trappers' census was the only technique that provided population estimates over all the northern forest in Saskatchewan. Trends in population size in each habitat for the period 1963-64 to 1967-68 were determined by summing the Conservation Area trappers' reports for each year.

If the census was incomplete in a given Conservation Area in any year the area was not included in the calculations. Resulting estimates provided trend information and not total numbers of beaver colonies. Census reports from the Athabasca were so incomplete that they were omitted entirely.

Each trapper reported his census to a Conservation Officer in the spring after termination of winter trapping. The census in many cases represented the number of colonies observed, and probably trapped, during that winter. In some cases it may actually have represented a better estimate of the previous year's population than that of the following year. It was however the only practical method of obtaining a population estimate from the trappers, most of whom were away from their traplines during the summer months. It was used in this report to represent an estimate of population size for the succeeding year.

Numbers of live colonies per square mile were determined from the plot surveys. Since this method (described in the following section) appeared to provide reliable counts, yearly densities of beaver colonies have been used in this thesis as an alternative source of estimating population changes in some habitats.

Determination of the Accuracy of the Trappers' Censuses

Census checks were carried out in nearly all habitats during the years of study. This was a continuation of a program started in the early years of the NFCA program. Originally most of the checks were conducted on the ground. Investigators travelled on foot or by canoe, tallied live colonies along watersheds and compared such counts to the trap-

per's submission. By the 1960's some aircraft time was made available for this work. Most checks were made from Cessna-180 and Beaver aircraft during late summer and fall periods. Criteria for distinguishing occupied colonies from unoccupied ones were the presence of a freshly-mudded house or a feed pile. These methods were employed in various habitats up to 1965.

A new method of determining the accuracy of the census was developed in 1964 and applied in a number of habitats in 1965, 1966 and 1967. It was developed because the ground technique was too time-consuming and costly and the aerial method usually resulted in some colonies being missed. The technique involved counting colonies in randomly selected plots 2 miles by 2 miles in size. Counts were made independently but at the same time by two observers in one aircraft operated at an altitude of between 500 and 1,000 feet. Repeated passes were made over each section of a plot until observers were sure all live colonies had been located. At the completion of each plot tallies were compared. Discrepancies in colony number or location were checked out. The method was utilized during the period between leaf-fall and freeze-up which usually coincided with the month of October in northern Saskatchewan.

Most survey plots were completed in the Churchill, Hyper-Churchill and Foster habitats and most of that work was carried out by personnel of the Department of Natural Resources at La Ronge, Saskatchewan.

Determination of Colony Composition

Numbers, sexes and ages of beaver in sample colonies were determined from both live-trapping and kill-trapping programs. Data for the Cub were

collected in the intensive study area and data for the Porcupine winter population were collected on the trapline of Peter Burym. Some additional live-trapping was carried out during summer months in Porcupine, Bronson and Foster habitats. Colonies were classified, according to the number of animals present, into one of the following types: family-group, pair or single-occupant. Family-group colonies contained adults and immatures, either kits or yearlings.

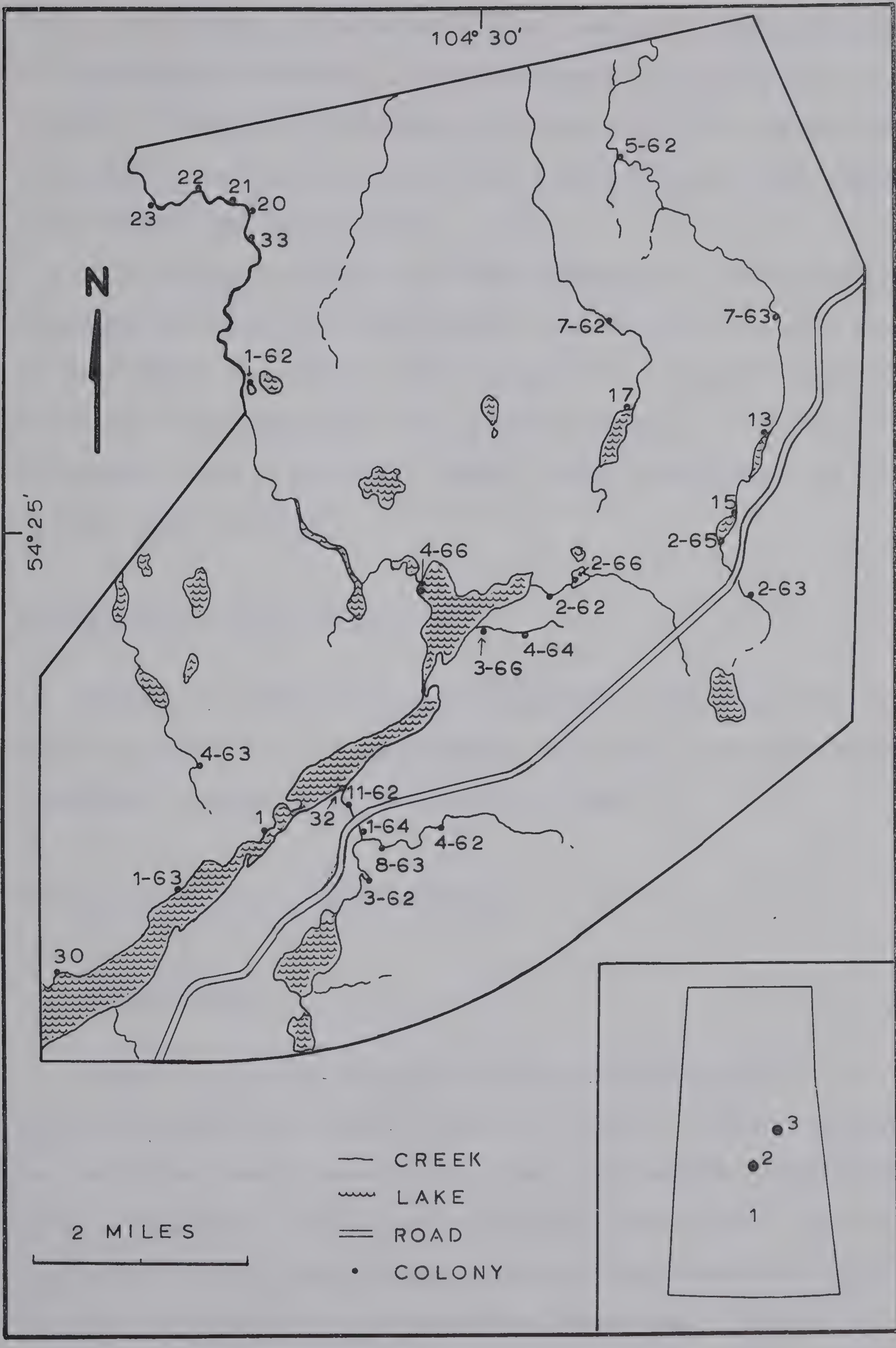
Determination of the Dynamics of the Cub Beaver

An intensive study was conducted in the Little Bear Lake area of Cub (Fig. 3) in which beaver at specific colonies were live-trapped, using both Bailey and Hancock traps, during September and October from 1964 to 1966. Traps were normally set during the afternoon and left until the following morning when they were checked. Beaver caught were measured, tagged in each ear with monel metal tags, style 1005, size 3 (National Band and Tag Company) and released. Circular, coloured plastic markers (Miller 1964) were attached to the tags to aid in recognition of swimming beaver and to enable trappers to detect tags on kill-trapped animals. Observations of beaver at night were made at some colonies.

It was my intention to observe the histories of some colonies on the intensive study area and to evaluate kill-trapping results after the fourth winter of occupation. For that reason colonies were originally assigned year-class numbers to correspond to the initial year of occupation (example 1-63; colony established in 1963). Criteria used to place colonies in year-classes were observations of numbers and sizes of beaver, beaver "signs" such as amount of cuttings, food cache size, lodge size,

Figure 3. The intensive study area in the Cub habitat showing locations of beaver colonies live-trapped and/or kill-trapped between 1964 and 1967.

1. Saskatchewan
2. Prince Albert
3. Location of study area


104° 30'
54° 25'
N
5-62
22
21
20
23
33
7-62
7-63
1-62
17
13
15
2-65
4-66
2-66
2-63
2-62
4-64
3-66
4-63
11-62
32
1
1-64
4-62
8-63
1-63
3-62
30
3
2
1
CREEK
LAKE
ROAD
COLONY
2 MILES

tracks, tooth marks; and estimated ages and numbers of beaver captured in live-trapping operations. For the purposes of this study it was not important to know whether a colony was present before the estimated year of occupation, as long as the colony was present since the year assigned as the initial year of occupation.

Kill-trapping was conducted at such colonies during the fourth winter of occupation as well as at other colonies on the study area whose year of establishment was unknown. Kill-trapping on the intensive study area was delayed until spring each year so that information on reproduction and survival could be collected. Numbers, sexes, measurements and ages of beaver were recorded.

Determination of Growth Rates

Beaver from sample kill-trapping operations on the Peter Burym trapline in Porcupine and from the intensive study area in Cub were weighed. Weights were recorded to an accuracy of 0.1 pound.

Measurements of Reproductive Performance

Field Collections

Trappers, provided with instruction and collection material prior to the spring trapping operations, removed and collected complete reproductive tracts from female beaver in the 4 years 1965 to 1968. Reproductive tracts were placed in plastic bags and frozen. Date of kill, location, site description and other pertinent information were recorded on labels. Trappers were reimbursed at the rate of $1.00 per tract. Collections were

made in 11 of the habitats as well as from the South-Saskatchewan. As an economy measure trappers were instructed not to collect tracts from all immature animals trapped. This was necessary since the bulk of the harvest consists of such animals. Conservation Officers and Game Management Officers of the Saskatchewan Department of Natural Resources assisted by organizing collections in their local areas and forwarding specimens to Prince Albert for examination.

Ovary Examination

Ovaries were fixed in Mossman's AFA, examined and preserved as described by Provost (1962). After fixation ovaries were sliced with a razor blade into transverse sections approximately 1 millimeter thick. The sections were not completely severed so that the overall form of the ovary would be preserved. Counts of corpora lutea of pregnancy were made macroscopically under a Lux-O-Magnifier Lamp. Numbers were recorded separately for left and right ovaries. After examination ovaries were stored in about 70 percent ethyl alcohol.

Corpora lutea are creamy white in colour in ovaries fixed in AFA and are large and conspicuous. They are even-sized in one ovary. Apparently, luteinized non-ovulated follicles do not typically occur in beaver (Provost 1958). In addition, polyovuly does not appear to occur in beaver since numbers of fetuses were never in excess of numbers of corpora lutea in any beaver in this study. I am confident, therefore, that all corpora lutea were counted and that the counts are good estimates of the numbers of ova released.

Counts of Fetuses and Resorptions

Fetuses in uteri were counted, removed and sexed when possible. Separate tallies were made for each side of the tract. Crown-rump measurements to the nearest 0.1 inch were made on all fetuses collected in 1967 and 1968. Resorbing fetuses were noted. In those cases where resorption was nearly complete the site of resorption was marked by a dark spot, and a small amount of yellowish material was usually present at that spot. Extreme vascularization and enlargement during late pregnancy probably resulted in scars of some early resorptions being missed in the count. During 1965, the first year of collections, some resorptions were probably missed due to my inexperience. For this reason data on resorption for that year have been omitted.

Sex Determination

Fetuses were sexed by macroscopic identification of the gonads which was possible only after about 30 days gestation. Sex was determined for live-trapped beaver beginning in 1966 when a holding cone (Whitelaw and Pengelley 1954) facilitated manipulation of live beaver in the field. The beaver sexing method of Rawley (1954) was used.

Sexes of kill-trapped beaver were determined and recorded on collection tags by trappers in a number of habitats. Since it had been determined that some Saskatchewan trappers guess at the sex of a beaver only those records were used that were submitted by trappers who were collecting reproductive tracts, who had become familiar with the internal sex organs of beaver and who collected mandibles from nearly all beaver trapped.

Age Determination

Mandibles of beaver were collected by trappers during winter and spring kill-trapping operations in the 11 habitats from which reproductive tract collections were made. Mandibles and female tracts from the same beaver were stored together. Large collections from both sexes for age structure determinations were made from eight habitats.

The dental technique developed by van Nostrand and Stephenson (1964) was employed in determining actual age of kill-trapped beaver. Criteria used to place beaver in age-groups were the advancement of closure of the root canals of the four cheek teeth and the number of summer and winter layers of cementum, primarily in the premolar. In the kit age-group the deciduous premolar is being replaced by a single-rooted permanent premolar. In yearlings the characteristic criteria used are the completely open root canals of the cheek teeth and lack of cementum. Two-year olds have a significant cementum development and closure is well advanced. The first layers of cementum are deposited in the third year of life. The age of beaver over the 2-year old group was determined by counting the number of winter layers of cementum, characteristically a lighter colour than the summer layers, and adding 2 years to that figure.

Van Nostrand and Stephenson based these criteria on dental development in 42 known-aged specimens from four locations in North America Confirmation of the accuracy of the technique has been provided by comparisons of the known age and dental age of beaver in other areas (Larson and van Nostrand 1968, this study). The technique was also developed for use in the Soviet Union (Kleinenberg and Klevezal 1966). The technique has replaced the use of less reliable methods, some of which were rev-

iewed by Patric and Webb (1960) and compared to the dental development technique by Larson and van Nostrand (1968).

Ages of live-trapped beaver were estimated using a combination of body weight and tail-width measurements as recommended by Rawley (1954). Ages of such beaver were recorded as kits (less than 1 year), yearlings (between 1 and 2 years), 2-year olds (between 2 and 3 years) and adults (over 3 years of age). This is the nomenclature recommended by Buckley and Libby (1955) and used by most authorities. Comparisons of estimated age with dental age after kill-trapping indicated that such estimates were highly reliable.

Determination of Trapping Intensity

During summer, 1967 beaver were live-trapped, tagged, sexed, aged and released in the Porcupine, Bronson and Foster habitats. Trappers in these areas, as well as areas in and around the intensive study area, were requested by letter to collect tags from kill-trapped tagged animals and forward them to their local Conservation Officer. To encourage the return of tags a payment of $1.00 was made per tag return.

Statistical Analysis

The distribution of Student's t was used to test for the significance of differences of ovulation rates, fetal rates, weights and numbers of beaver in colonies. Sex ratios were tested using the Chi-square distribution.

Ages of animals collected from the Foster habitat were biased since yearlings consistently outnumbered kits. It was apparent that trappers in

this remote, northern habitat were not collecting all kit mandibles presumably thinking that it was hardly worthwhile aging what was obviously a kit beaver. The exponential equation, $\text{Log } Y = 1.8774 - 0.1127X$ was computed from the remaining Foster age distribution. The Y value for $X = 1$ was then calculated and that number was used for the kit age-group. The total was then adjusted.

I considered differences to be significant when probability values were equal to or less than 0.1. Confidence limits were calculated at 95% to conform to standard practise.

RESULTS

Harvests and Population Changes

The Harvest: 1946 to 1967-68

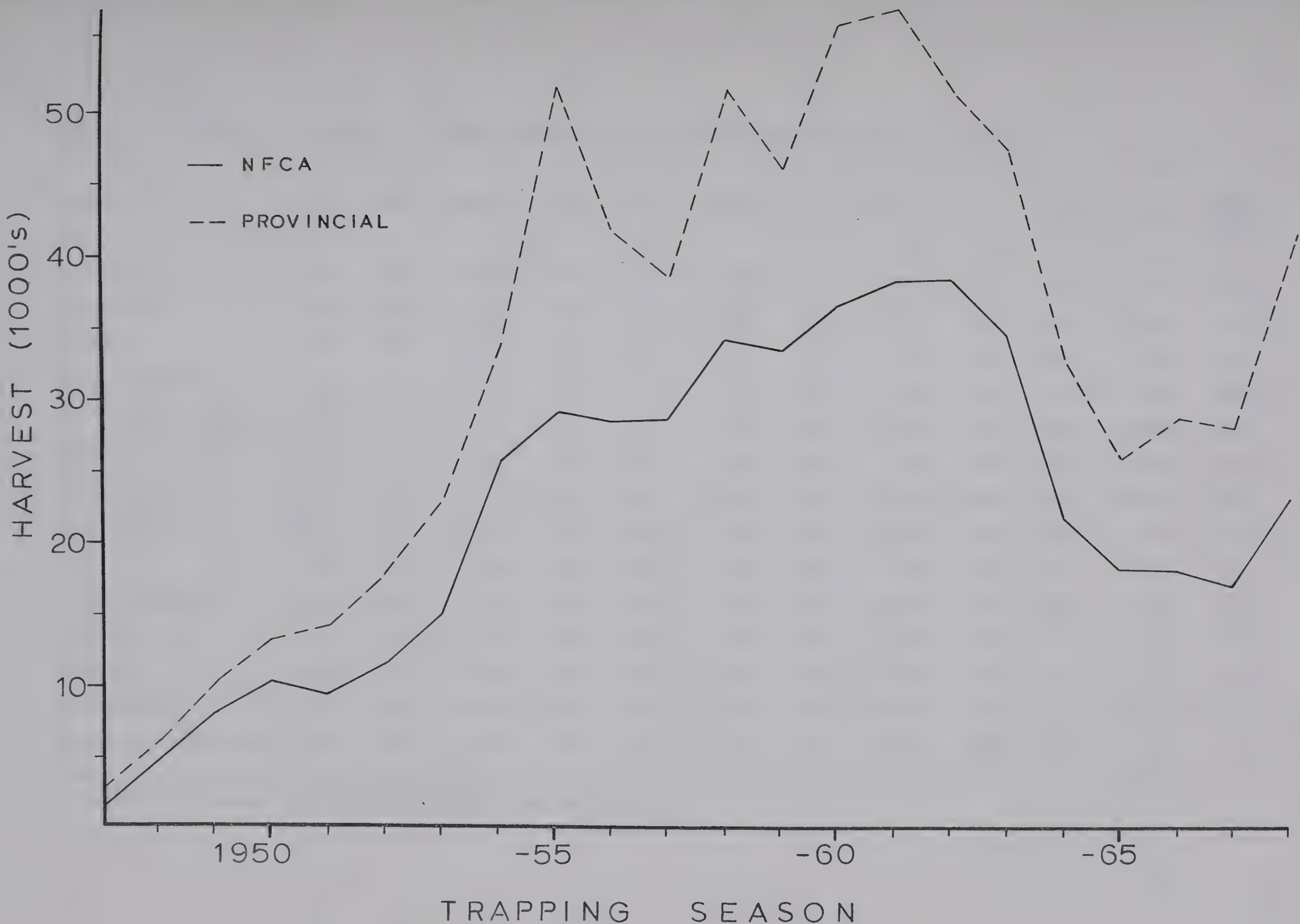
Harvests of beaver in both Saskatchewan as a whole and the NFCA rose steadily to about the 1961-62 season and then began to decline (Fig. 4). Major declines were experienced in the Pasquia, Meadow Hills, Mostoos, Manitoba Lowland, Prince Albert Uplands, Churchill and Hyper-Churchill habitats (Table 1). Harvests in the two habitats, Churchill and Hyper-Churchill, declined by over 10,000 animals during the period 1959-60 to 1963-64 (Table 1). Major harvest declines were in phase, occurring in 1963-64 and 1964-65. Most other habitats experienced somewhat lower harvests during that period. Harvests increased in all habitats in 1967-68.

Population Changes: 1946 to 1963-64

In the early years of the NFCA harvests were low (Fig. 4) suggesting a very low population size during that period. Gradual, but very substantial increases in harvest during the 1950's suggests a parallel increase in the abundance of beaver. These observations indicated that the beaver in the northern forest were increasing in numbers from 1946 to about 1960.

Major declines in harvest size in some habitats in the 1960's suggested that the population was declining during that period in those areas. Generally a slight decline in numbers of colonies was reported by trappers

Figure 4. Harvests of beaver in Saskatchewan: 1946-47 to 1967-68.



NFCA
PROVINCIAL
HARVEST (1000's)
50
40
30
20
10
1950
-55
-60
-65
TRAPPING SEASON

Table 1 Harvests of beaver in Saskatchewan habitats between 1958-59 and 1967-68

Habitat	58-59	59-60	60-61	61-62	62-63	63-64	64-65	65-66	66-67	67-68	Mean	Mean/Area *
Pasquia	2364	2927	3686	3716	2730	2188	1341	1765	1401	2372	2449	0.94
Porcupine	1348	1998	2926	2707	2901	2266	1846	1950	2293	3054	2333	0.86
Bronson	544	830	1057	1259	1182	1381	639	918	1138	1365	1031	0.86
Meadow Hills	981	1247	1441	1368	1183	1139	585	710	880	1310	1084	0.60
Manitoba Lowland	2401	2381	3120	3101	2955	2255	1530	1258	1294	1599	2189	0.35
Mostoos	1766	2173	2094	2325	1871	787	668	790	928	1313	1472	0.34
Churchill	12335	13826	13182	11259	11417	4851	5683	5379	4586	7184	8970	0.33
P A Uplands	2842	3042	2931	3112	2016	1776	811	989	956	1283	1976	0.25
Cub	493	609	626	745	783	784	391	403	507	581	592	0.19
Hyper-Churchill	2625	2763	2267	2394	2256	943	831	804	749	1170	1710	0.17
Uranium City	190	360	159	246	325	194	268	155	173	381	245	0.14
Foster	1516	1125	977	971	912	832	1047	793	560	744	948	0.09
Athabasca	1167	1577	1352	1592	1293	1338	1087	1058	497	919	1188	0.04
Northern Transition	364	447	369	470	410	414	392	362	262	516	401	0.02

* number of beaver harvested per square mile per year

in those same habitats. Some checks along well-travelled water routes in Churchill in 1962 and 1963 showed the trappers' census to be grossly over-stated. It appeared that trappers were reluctant to report fewer colonies because of expectations of lower harvest limits. There seemed little doubt that substantial reductions in the numbers of beaver occurred in at least Churchill, Hyper-Churchill and some other habitats.

Accuracy of the Trappers' Census: 1964 to 1967

The results of ground and aerial methods of survey (Table 2) in the Churchill, Hyper-Churchill and Foster habitats in 1964 and 1965 indicated wide variation in the accuracy of individual trapper's census. These surveys also revealed the presence of beaver in remote areas of Foster that were not censused and presumably were trapped lightly or not at all.

The intensive plot surveys from 1965 to 1967 in the same three habitats suggested a general trend to greater under-estimation of population size during that period with the exception of Hyper-Churchill, where trappers continued to report more colonies than actual, at least until 1967. Analysis of the raw plot data by Conservation Area showed that trappers in some Areas such as N-7 and N-9 were consistently accurate while trappers in others were consistently inaccurate. The plot surveys also revealed non-censused populations in remote areas of Athabasca, Uranium City and Northern Transition habitats.

Population Changes: 1963-64 to 1967-68

The trappers' census (Fig. 5) indicates that populations during the study period increased in Meadow Hills, Churchill and Hyper-Churchill

Table 2 Saskatchewan trappers' beaver census compared with ground, aerial and plot surveys: 1964 to 1967

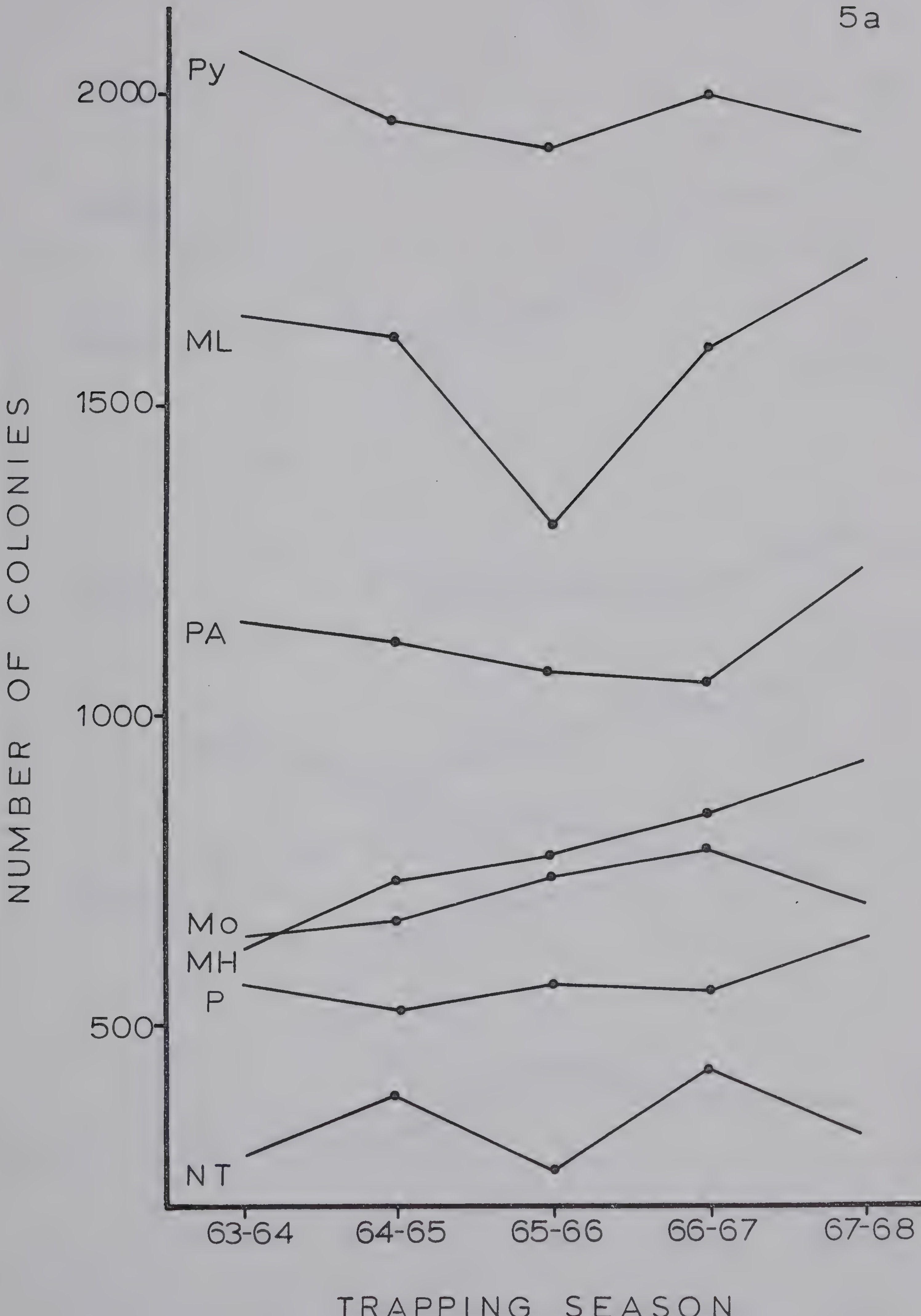
Habitat	Area	Year	Survey Type	Trappers Count	Survey Count	Difference
Churchill	N-33	'64	G	38	66	+28
	N-8 (7)	64	G	0	14	+14
	N-11	64	G	12	12	0
	N-9 (5)	65	G	23	17	- 6
	N-9 (13)	65	G	22	25	+ 3
	N-8 (2)	65	G	27	22	- 5
	N-79 (6)	65	G	6	5	- 1
	N-7 (3)	65	G	8	5	- 3
	Grouped	65	P	119	134	+15
	Grouped	66	P	194	198	+ 4
	Grouped	67	P	168	235	+67
Foster	N-79 (7)	64	G	0	8	+ 8
	N-79 (7)	64	A	0	9	+ 9
	N-11 (7)	65	G	0	10	+10
	N-78 (3)	65	G	18	13	- 5
	Grouped	65	P	46	45	- 1
	Grouped	66	P	63	73	+10
	Grouped	67	P	42	74	+32
Hyper-Churchill	N-6	64	G	21	32	+11
	N-5	65	G	9	6	- 3
	N-5 (1)	65	G	25	18	- 7
	Grouped	65	P	45	27	-18
	Grouped	66	P	50	32	-18
	Grouped	67	P	36	44	+ 8
Athabasca	N-19	66	P	10	6	- 4
	N-22	67	P	6	14	+ 8
Mostoos	N-21	64	G	22	40	+18
	N-21	64	A	7	7	0
	M-37	66	P	8	16	+ 8
	Grouped	67	P	50	64	+14
Northern Transition	N-24	66	P	4	9	+ 5
Uranium City	N-23	66	P	7	21	+14
	N-23	67	P	6	42	+36
Bronson	M-47&-56	66	P	20	27	+ 7
P A Uplands	P-72	65	A	118	180	+62
	P-36	65	A	54	51	- 3
	P-20	65	A	45	43	- 2

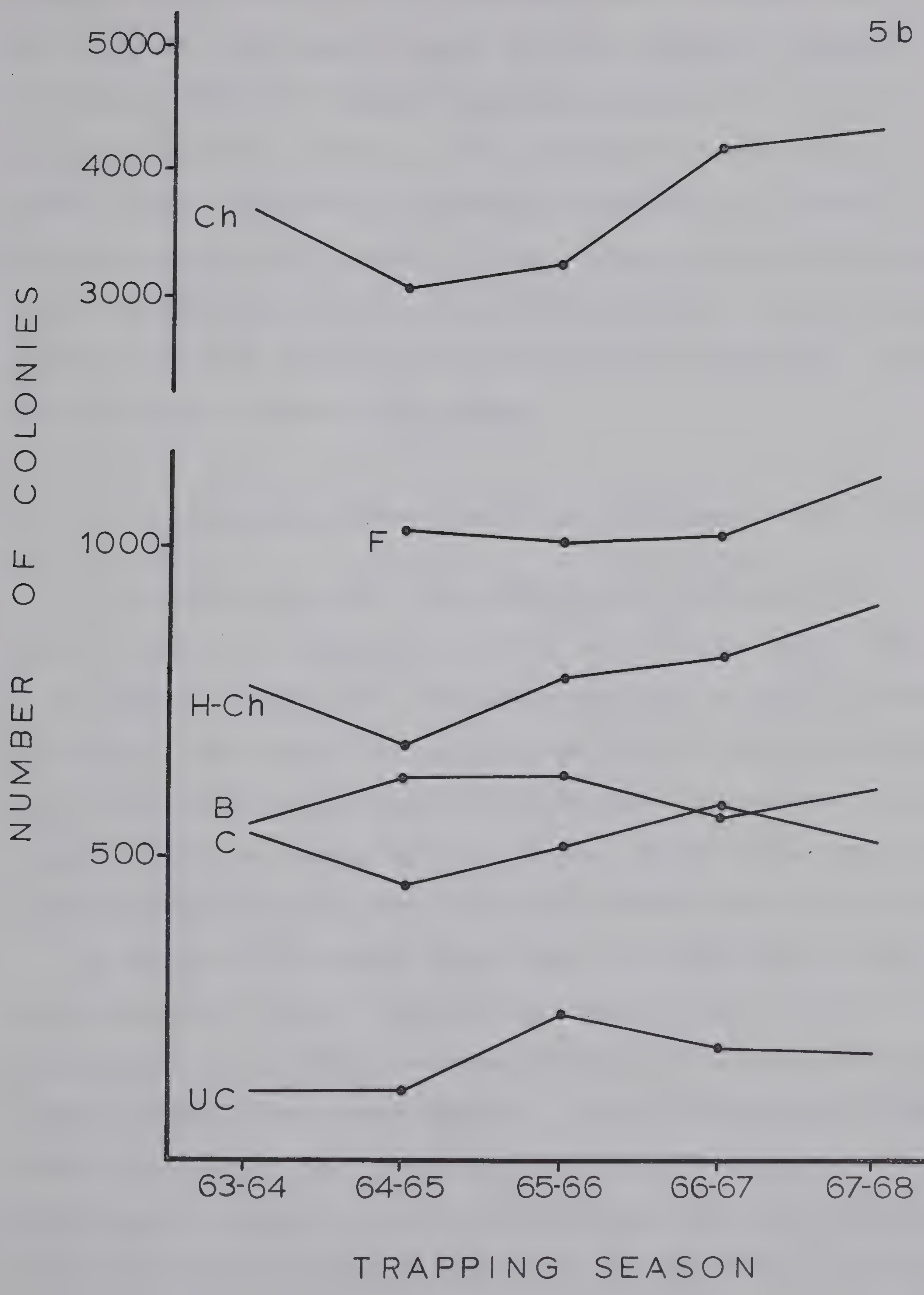
G=Ground; A=Aerial, other than plot; P=Plot (7)=trapline number

Figure 5. Trends in population size as indicated by the trappers' census. Data indicate trends only. Some incompletely censused Areas have been omitted.

a) Pasquia, Porcupine, Meadow Hills, Prince Albert Uplands, Manitoba Lowland, Mostoos and Northern Transition habitats.

b) Bronson, Cub, Hyper-Churchill, Churchill, Foster and Uranium City habitats.


5a
NUMBER OF COLONIES
2000
1500
1000
500
Py
ML
PA
Mo
MH
P
NT
63-64
64-65
65-66
66-67
67-68
TRAPPING SEASON


5b
NUMBER OF COLONIES
5000
4000
3000
1000
500
Ch
F
H-Ch
B
C
UC
63-64
64-65
65-66
66-67
67-68
TRAPPING SEASON

and were somewhat stable in Porcupine, Bronson, Cub, Uranium City, Northern Transition and the two Conservation Areas of Pasquia (H-44 and H-105) for which complete census data were available. Results of plot surveys (Table 3) indicated increasing populations in Churchill and Hyper-Churchill as well as a modest increase in Foster, and suggested a stable population in the Mostoos and Uranium City habitats between 1966 and 1967. A sudden decline in population size in Manitoba Lowland in 1965 followed by an equally rapid increase in numbers during 1966 and 1967 (Fig. 5) was reported by the trappers of that area. Those estimates were not confirmed by surveys.

Factors Influencing Harvests and Population Changes: 1946 to 1963-64

In the very early years of the NFCA program rigid control over beaver trapping kept the harvest of beaver at a minimum. Beaver were a new commodity in many areas and trappers were slow to learn the methods of capture. Many trappers who did not have dogs in those years travelled on foot and carried little equipment and supplies. The relative inefficiency of the harvest during the first 10 years of the program contributed to the apparent unimpeded beaver population increase during that period.

By the mid 1950's harvest limits became less restricting. Quotas were liberalized, seasons lengthened and trappers through their Area organizations and government education programs were becoming more knowledgeable and efficient beaver trappers. Scattered occurrences of beaver die-off's in the mid 1950's prompted the further liberalization of harvest restrictions. The snare, the Conibear trap and tracked over-snow vehicles were introduced to Saskatchewan trappers in the late 1950's. Snow veh-

Table 3 Number of beaver colonies per square mile of habitat (calculated from plot survey results)

Habitat	1965	1966	1967
Churchill	0.80 (42)*	0.83 (60)	0.98 (60)
Foster	0.59 (19)	0.65 (28)	0.66 (28)
Hyper-Churchill	0.52 (13)	0.62 (13)	0.85 (13)
Athabasca		0.38 (13)**	
Mostoos		0.67 (6)	0.67 (24)
Northern Transition		0.28 (8)	
Uranium City		0.88 (6)	0.88 (12)
Bronson		1.13 (6)	

* number of plots in parenthesis
** 1965 and 1966 data combined

icles rapidly became popular, especially in the southern habitats, and enabled larger areas to be covered and more traps to be set out. Harvests continued to increase. During this period a booming northern human population and a lack of employment resulted in more and more trappers taking to the field. This situation was soon followed by declines in harvest.

Factors Influencing Harvests and Population Changes: The Study Period

A number of Conservation Areas in Churchill and Hyper-Churchill were closed to beaver trapping in 1963-64. All Areas were opened to beaver trapping the following year, but quotas in most were small. This had the effect of discouraging some trappers during that period. About the same time mining operations started in the La Ronge area which further reduced the numbers of trappers operating in Churchill and Hyper-Churchill by providing alternative employment.

Trappers in at least the Porcupine, Bronson, Meadow Hills, Cub and southern Areas of the Pasquia habitat remained active during the study period. Trappers in several areas of Manitoba Lowland in 1964-65 reported unusual numbers of dead beaver. This was accompanied by similar reports from adjacent areas of the province of Manitoba (D. Miller, Manitoba game biologist personal communication).

Relationship Between Harvest and Population Change

The years of largest harvests, the late 1950's were soon followed by unconfirmed, but seemingly substantial reductions in the numbers of beaver. During the period of study when harvest limits were reduced

in a number of habitats and harvests were correspondingly small, population increases were reported by trappers and confirmed by the plot surveys. Major declines in harvest in the mid-1960's and the population increases between 1965 and 1967 occurred in the same habitats.

Harvest Per Square Mile: A Rating of Habitats

The following grouping of habitats is based on the number of beaver harvested per square mile (Table 1).

Beaver Harvested Per Square Mile Per Year	Habitats	Rating
0 - 0.24	C, F, UC, A, NT, H-Ch	Low
0.25 - 0.49	Mo, Ch, ML, PA	Mediocre
0.50 - 0.74	MH	Moderate
0.75 - 0.99	P, Py, B	High

Differences in harvest between habitats are a result of variations in beaver densities and trapper effort. For much of the 10-year period trapper effort was reasonably similar with the possible exceptions of the very northern habitats where effort was likely somewhat less. These variations in harvest are considered, then, to be primarily due to variations in population abundance which reflect habitat quality. These groupings will be referred to in this thesis as quality groupings.

Colony Composition

Colony Types

Three types of colonies were found in live- and kill-trapping

operations (Table 4). The greatest proportion of colonies with one beaver trapped was found in the early summer live-trapping in Porcupine about a month following the termination of the commercial harvest. The majority of these colonies were probably single-occupant colonies (see section, single-occupant colonies). After 3 years of trapping in the intensive study area in Cub, the proportion of colonies with one beaver increased and the proportion of family-group colonies declined. The mean proportion of colonies with one beaver declined from summer to fall to winter period. The proportions of colony types did not vary significantly between Porcupine and Cub during the winter period.

Family-group Colonies

The mean number of kits kill-trapped in colonies in Porcupine was significantly greater than in Cub ($P<0.05$)(Table 5). There were also significantly more yearlings in Porcupine colonies than in Cub colonies ($P<0.05$). Two-year olds were trapped at two family-group colonies in Porcupine where adults were present. This was not found in either live-trapping or kill-trapping in Cub. In addition, one colony in Porcupine contained three adults. The maximum number of adults found in Cub colonies was two. The mean number of beaver kill-trapped per family-group colony in Porcupine was significantly greater than in Cub live-trapping ($P<0.05$) and Cub kill-trapping ($P<0.01$). In no cases were the ages of adults in family-group colonies separated by more than 3 years (Table 6).

Pair Colonies

In no pair colony trapped were the two beaver of the same sex

Table 4 Proportions of colonies with one, two and more than two beaver trapped in various habitats

Period	Habitat	n	Number of Beaver Trapped 2+*	2	1
Summer (Live-trapping)					
June, 1967	Porcupine	13	30.8	7.7	61.5
July, 1967	Bronson	6	50.0	16.7	33.3
August, 1967	Foster	4	75.0	25.0	
	Mean	23	43.5	13.0	43.5
Fall (Live-trapping)					
1964	Cub	10	70.0	20.0	10.0
1965	Cub	12	58.3	8.3	33.3
1966	Cub	13	53.8	7.7	38.5
	Mean	35	60.0	17.1	22.9
Winter (Kill-trapping)					
1965 to 1967	Cub	26	57.7	26.9	15.4
1967-68	Porcupine	20	60.0	20.0	20.0
	Mean	46	58.7	23.9	17.4

* 1=one beaver trapped; 2=two beaver trapped; 2+=more than two beaver trapped or presence of kits (family-group colonies)

Table 5 Mean numbers of beaver trapped per colony in two habitats

Colony Type	Age-group	Cub FL-t			Cub WK-t			Porcupine WK-t		
		$\bar{x}$	r	n	$\bar{x}$	r	n	$\bar{x}$	r	n
Family-group	Kits	2.0	0-3*	20	1.9	1-3	15	3.0	1-5	12
	Yearlings	1.5	1-2	10	1.1	1-2	7	2.1	1-3	8
	2-year olds	0			0			1.0		2
	Adults	1.2	0-2	22	1.3	0-2	16	1.2	0-3	12
	All ages	3.8	2-6	22	3.6	2-5	16	5.8	2-10	12
All Types	All ages	2.9	1-6	35	2.8	1-5	26	4.1	1-10	20

FL-t=Fall Live-trapping; WK-t=Winter Kill-trapping; n=number of colonies

* values of 0 are included; ie, if 0 kits were trapped at a colony where kits were known to be present, it was included in the sample

Table 6 Ages of beaver in a) adult pairs of family-group colonies, b) pair colonies, and c) single-occupant colonies

Colony Type	Habitat	Colony Number	Age (estimated*, dental) Male	Female
Family-group	Cub	15	5	5
		21	7	6
		22	12	12
		4-62	11	9
		5-62	8	10
		7-62	7	5
		2-63	7	7
		4-63	15	12
	Porcupine	PB-45	10	11
		PB-47	9	10
		PB-48	9	7
		PB-49	11	10
		PB-58	12	10
Pair	Cub	17	2½	3½
		20	2½	6
		23	5	8
		33	9	6
		1-62	1½	2½
		11-62	Adult*	Adult*
		2-65	2½	2½*
		2-66	?	2½*
		4-66	2½*	2½*
	Porcupine	PB-12	11	4
		PB-15	2½	2½
		PB-43	2½	1½
		PB-46	4½	3½
Single-occupant	Cub	13		Adult*
		32		3½
		8-63	1½	
		4-64	5½&6½	
		3-66		1½*
		P-5-4		1½*
		P-7-1	2½*	
		P-7-2	1½*	
		P-7-4		1½*

?=observed only
* estimated from measurements at live-trapping

(Table 6). Two-year olds were present in eight of the 13 pair colonies. Yearlings were present in two pair colonies. The ages of adults in pair colonies were more widely separated than those of adults in family-group colonies.

Single-occupant Colonies

Some of the sites where one beaver was live-trapped in Porcupine had the following characteristics. The area flooded was small and shallow. Lodges were newly constructed and tiny. Such characteristics suggested recent occupancy by one beaver commencing after spring breakup. Similar sites where one beaver was live-trapped were found in the intensive study area during fall months. Lone beaver were also trapped in previously occupied sites.

Ages of beaver in single-occupant colonies indicated a preponderance of young animals (Table 6). Three yearlings and a 2-year old were trapped at the small pondsites in the Porcupine habitat during June, 1967. In the intensive study area during fall two of the five single-occupant colonies were established by yearlings, the remainder by adults.

Beaver of the Intensive Study Area

During the live-trapping in the intensive study area 88 individual beaver were captured a total of 136 times. Eleven beaver were captured in each of 2 years. Only one beaver was captured in each of the three live-trapping programs. In the kill-trapping 74 beaver were taken.

The history of some of the colonies of the intensive study area

between 1964 and the 1966-67 trapping season is illustrated in Figure 6. Columns headed 64, 65 or 66 refer to fall live-trapping in those calender years. Columns headed 64-65, etc. refer to winter kill-trapping which removed animals from the population. Locations of these and other colonies cited in this section are shown in Figure 3.

Number of Beaver in Colonies

The mean number of beaver trapped at colonies in the intensive study area were shown in Table 5. The greatest number of beaver trapped at any colony during the period was six. In some colonies such as 1 (1964) and 13 (1964) where six beaver were live-trapped at each colony some additional animals were missed. The maximum number of beaver present at any one colony during the period of investigation was probably eight. Not more than three age-groups of beaver were present at one colony. Most family-groups appeared to number about five or six beaver.

Movements of Beaver

Movements of family-groups were common during the study period. Beaver were forced to move short distances either downstream or upstream to find suitable supplies of hardwoods for winter storage. An example of such yearly movements was colony 4-63, which moved downstream about 400 yards in the summer of 1964, and another 1,200 yards in the summer of 1965. Similar yearly movements were observed at many other colonies. Other family-groups such as 3-62, 5-62, 7-63 and 1-64 remained in the same general area, but shifted from one adjacent dammed area to another each year.

Figure 6. Beaver at specific colonies in the intensive study area between 1964 and 1966-67.

a) colonies 1, 13 and 2-62

b) colonies 3-62, 2-63, 4-63 and 7-63

A = colony alive, but not trapped

D = colony dead

O = kit

θ = yearling

⊕ = 2-year old

● = adult

⓪ = trapped at another location

X = killed

--- = estimated period of animal's presence

L-t = live-trapped

K-t = kill-trapped

6a

COLONY	TAG NUMBERS		L-t 64	K-t 64-65	L-t 65	K-t 65-66	L-t 66	K-t 66-67
1	5	6	♂	♂				
	9	10	♂	♂				
	37	38	♂	♂				
	7	8	⊖♀	– – – –	– – –		(●♀)	(●♀)
	3	39	⊖					
	1	4	●♀	●♀				
				⊖♀				
	146	157			○			
	148	149			♂		⊖♂	
	184	185			○			
	180	181			●			
	182	183			●			
13	51	52	♂	♂				
	41	42	♀	♀				
	43	44	○					
	45	46	⊖				D	
	47	48	⊖♂	⊖♂				
	49	50	●♀		●♀			
				●♂				
2-62	19	20	○					
	60	61	○			(⊖)		
	62	63	♀		⊖♀	⊖♀		
	15	16	⊖					
	17	18	●					
	21	22	●					
	153	154			●			
						♀		
							~~♂~~	
	201	202					♂	♂
	203	204					♂	♂

6b

COLONY	TAG NUMBERS		L-t 64	K-t 64-65	L-t 65	K-t 65-66	L-t 66	K-t 66-67
3-62	55	56	○	– – – – –	– –	⊖		
	80	81	♂	– – – – –	– – –	♂		
	82	83	○					
	57	58	⊖					
	116	117	– – –	– – – –	♀	– – – – –	– – – –	♀
	118	119	– – –	– – – –	♂	– – – – –	♂	
					– – – –	♀		
					– – – –	♂		
	211	212					♀	
	213	214					♂	
	243	244					♀	
2-63	68	69	○					
	70	71	○					
	64	65	♀	– – – – – – –			♀	♀
	66	67	♂	– – – – – – –			– – –	– – ♂
	101	102			⊕			
	231	232					♀	♀
	233	234					♂	
	235	236					♂	♂
4-63	124	125	– – –	– – – –	⊖			
	120	121	– – –	– – – –	♀		♀	♀
	122	123	– A	– – – – –	♂		♂	♂
	217	218					♀	♀
	219	220					♂	♂
	221	222					♀	♀
7-63	135	136			♀		♀	
	137	138			♂		♂	♂
	130	131	– A	– – – – –	⊖			
	133	134	– –	– – – – –	⊖			
	245	246					♂	♂
	247	248	– – –	– – – – –	– – – –	– – – –	♀	♀
								♀
								♂

The family-group present at colony 2-63 in 1964 was not at this colony-site in 1965 during the live-trapping nor were they at any other colony-site in the immediate area. A lone 2-year old was live-trapped and observed at night at the site in 1965. This animal was in the process of storing food for the winter. In 1966 the two adults had returned and produced a litter of three kits (Fig. 6). In my opinion this family was not present in the study area in 1965.

A number of tagged family-groups moved out of the area including 1-63, 30 and the second family at colony 1. Colony 1-63 was established in 1963 and two adults and a kit were tagged in fall, 1964. In fall, 1965 the site was not occupied despite the fact that the colony had not been trapped. In fall, 1965 two kits, a yearling and an adult were trapped and tagged at colony 30. These beaver had not been at this site in 1964. The colony was not trapped in 1965-66, but the site was not occupied in fall, 1966.

In 1965 a new family-group of adults and kits moved into colony 1 (Fig. 6). The origin of this group is unknown. In 1966 only one member of this new group was present at colony 1 even though the colony was not kill-trapped the previous spring. Beaver "signs" at the colony-site suggested that not more than one beaver was present.

Emigration of Immature Animals from Parental Colonies

At most colonies live-trapped 2 years in succession, and not kill-trapped, some of the original kits were missing during the second fall. Calculated frequency of dispersal from five colonies was 60 percent of the original kits. It is unlikely that these yearlings were merely

absent from the colony during the period of live-trapping which was conducted during the month prior to freeze-up. Animals returning to winter with their parents would have to do so before freeze-up. In addition, two yearlings, originally tagged as kits in 1964 were trapped on adjacent traplines during the 1965-66 season. They were beavers 55,56 of 3-62 and 60,61 of 2-62 (Fig. 6). Thus both of these animals had left their parental colonies in their second summer of life. Both had travelled between 50 and 75 miles to get to the locations where they were kill-trapped, assuming their routes were by water.

Animals captured as yearlings were never recaptured at the same colony the following year (Fig. 6). Obviously those immatures that spent two complete years with the family-group left the parental colony during their third summer of life.

Survival and Loss of Young Beaver on the Intensive Study Area

Beaver are born at or shortly after spring break-up, which occurs normally in mid-May in the intensive study area. The open-water period in the area is about 5 months in duration, from about mid-May to late October. At ten colonies that were live-trapped during one of the three fall periods and kill-trapped the following spring, 28 kits were known to have survived to the fall. Assuming that the birth rate at these ten colonies equalled the mean of the Cub habitat for that period (2.88 per female, Appendix III) a survival of 97.3 percent is indicated. Loss, then, during the first 5 months of life is low.

At the same ten colonies 22 kits were kill-trapped during the March-April kill-trapping when they would have been about 10 to 11 months of age. Some kits may have been missed in the spring trapping. Minimum survival during the period October to March-April was 81.5 percent. Maximum loss was 18.5 percent during the winter prior to the spring trapping period.

At six colonies live-trapped during 2 consecutive years in which kits were present during the first year, and at which no kill-trapping took place during the winter of the first year, six of 15 original kits were caught. This is a minimum survival of 40.0 percent of the number of kits alive at 5 months of age during the period 5 months to 17 months of age. Since I have already calculated a loss of 18.5 percent during the period from 5 to 11 months of age, calculated loss during the second open-water period was 41.5 percent (60.0 - 18.5). Loss during this latter period includes both mortality and emigration. It has already been shown that some animals in their second summer of life dispersed from parental colonies in this area.

Years of No Reproduction

Since neither kits in 1965 or yearlings in 1966 were present at colony 4-63 it appears that no litter was successfully raised in 1965. Similarily, at colony 2-63 the absence of the family-group in 1965 and of yearlings in 1966 is strong evidence that no litter was raised in 1965.

Kill-trapping and Colony Composition

At colony 13 (Fig. 6) and at another colony in 1963-64 the adult male was removed in late-spring kill-trapping, but the adult female

was left. Both females should have been bred prior to removing the male. In subsequent trapping operations during the following year both females were captured. They both appeared to be without kits.

Single-occupant colonies were established by beaver originating from colonies that were kill-trapped. One of the original yearlings of colony 1 was trapped in a small single-occupant colony in 1966 at a location about 1 mile distant from the parental colony. Its age was established at 3½-4 years following its removal during the 1966-67 trapping season. The adult female at colony 13 appeared to remain as a lone occupant for 1 year following removal of most of the original family.

Harvest Following the Fourth Summer of Colony Occupation

At six colonies established in 1962 or earlier the number of beaver kill-trapped in 1966 averaged 3.0 per colony. The mean harvest in 1967 at three colonies established in 1963 was 4.7. This is a harvest equivalent to 1.2 beaver per colony per year.

Some Spring Observations at Colony 2-63

At colony 2-63 virtually all the water had disappeared by February, 1967. Observations during kill-trapping in March and April showed that the lodge was not being used as it had been left high and dry and exposed to the cold winter air beneath the ice. Signs of feeding around the food cache were present but were limited. Inspection of the pondsite after trapping ended in May showed that the beaver had constructed small burrows in the exposed dam. Bankruns were not present at this colony.

Four of the five beaver originally tagged at the colony-site during the preceding fall were kill-trapped following refilling of the pond by melt water during the warmer days of early May. Examination of the pregnant female showed the presence of four fetuses about three-quarters developed. This female had raised two young at the colony-site in 1964 and three young in 1966. In addition, body weights of the beaver were maintained. The adult female had gained 1 pound since being weighed in September and the two kits that were kill-trapped had a combined weight increase of half a pound.

Growth

Mean weights of Porcupine beaver kill-trapped in spring ranged from 17.5 pounds for kits to 49.3 pounds for the 5 to 8 year age grouping (Fig. 7). In Cub mean weights increased from 14.3 pounds for kits to 41.1 pounds for the 9 to 12 year grouping. Two animals older than 12 years in the Cub sample averaged 32.8 pounds suggesting a decline in old age. Mean weights of beaver from Porcupine were significantly greater than those from Cub in all age-groups (at 90 % in 3½ comparison). Overlaps of weight ranges occurred between all consecutive age-groups in both habitats.

Reproduction

Ovulation Rates

Four-year mean ovulation rates of beaver ranged from 5.27 ± 0.61 in the South-Saskatchewan to 3.00 ± 0.63 in the Uranium City habitat (Fig. 8 and Appendix II). Mean ovulation rate of all 398 counts was 4.56.

Figure 7. Body weights of beaver by age in the Porcupine and Cub habitats: sexes combined

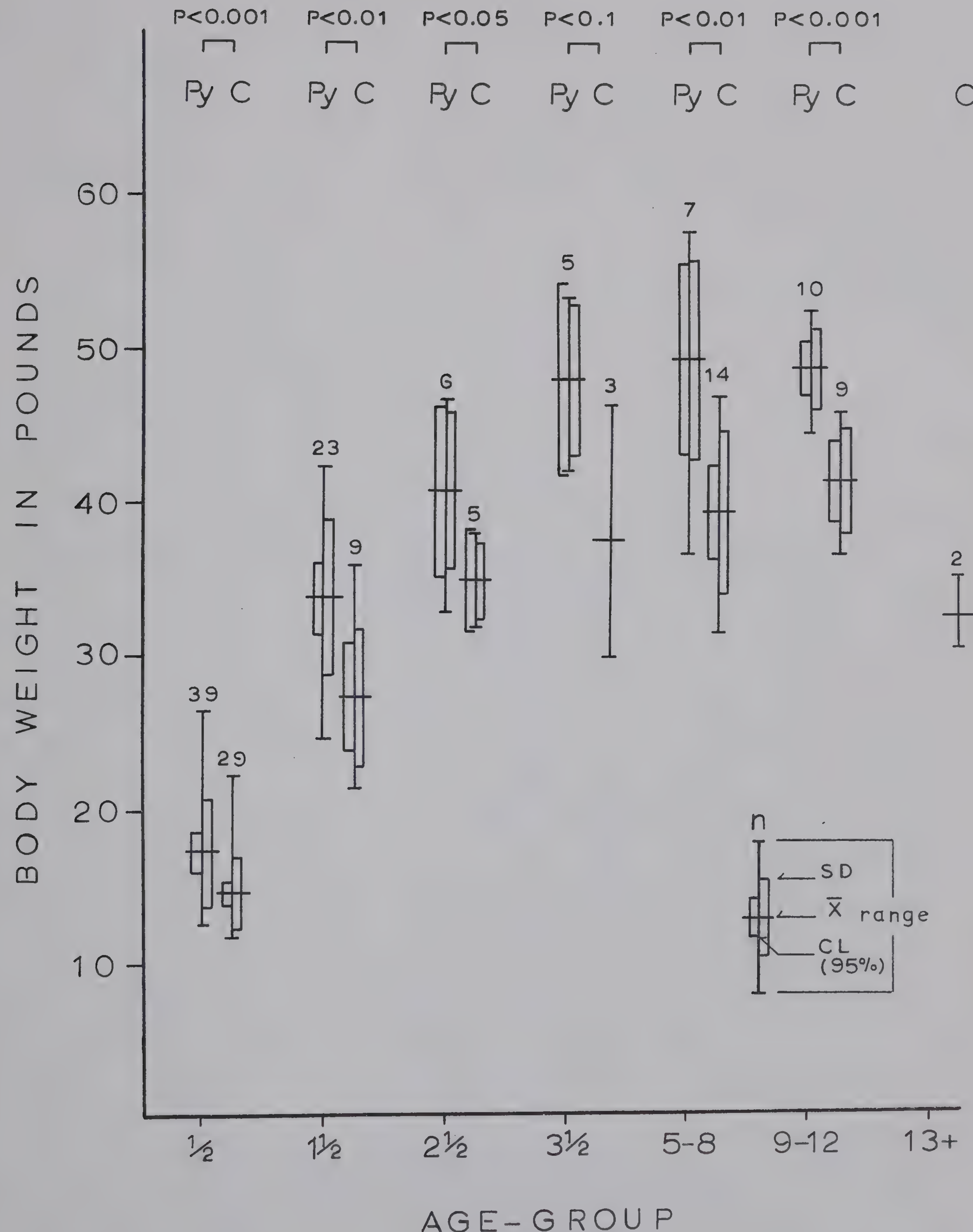
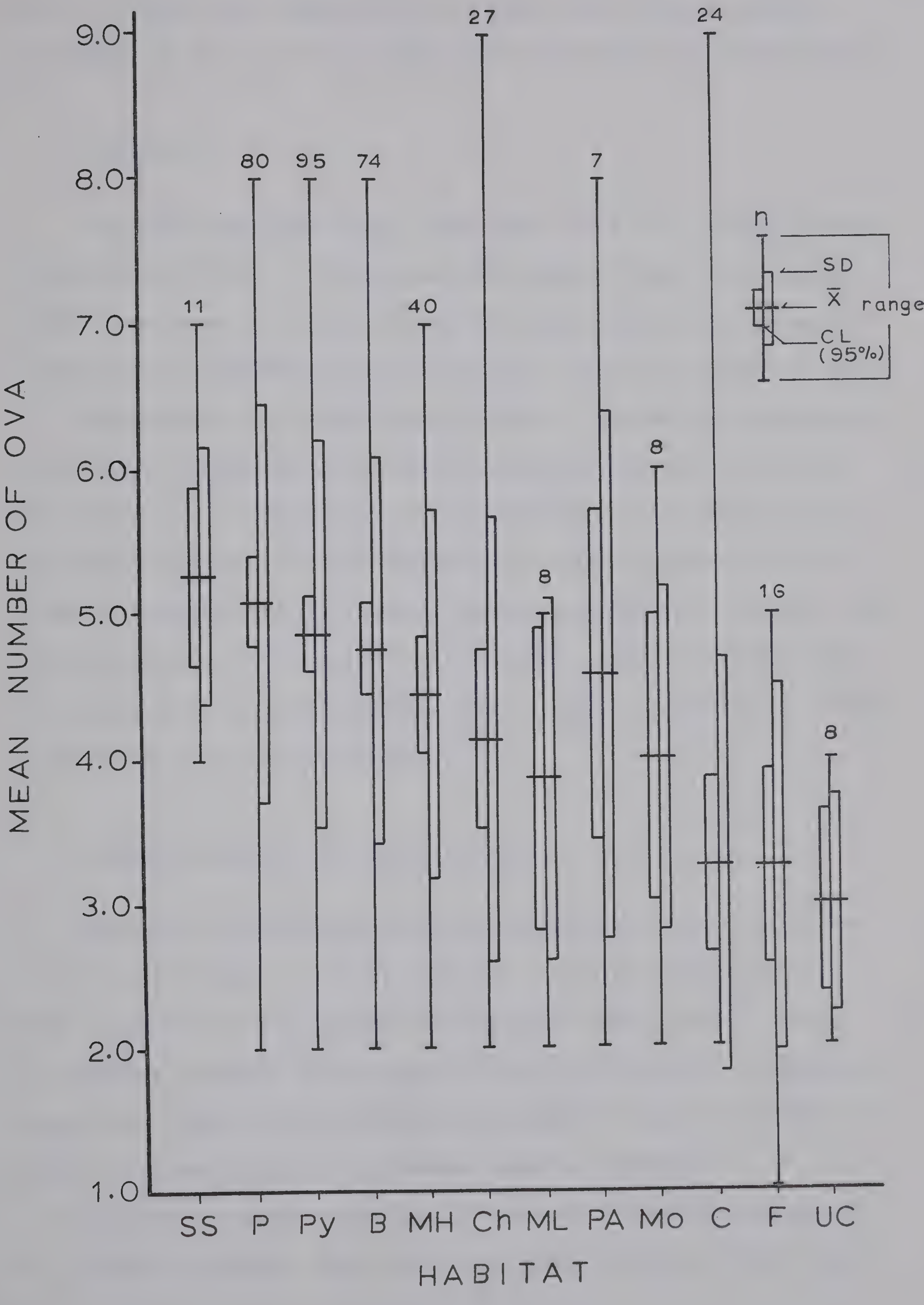

P<0.001
P<0.01
P<0.05
P<0.1
P<0.01
P<0.001
Py C
Py C
Py C
Py C
Py C
Py C
C
BODY WEIGHT IN POUNDS
60
50
40
30
20
10
39
29
23
9
6
5
5
3
7
14
10
9
2
n
SD
$\bar{X}$
range
CL
(95%)
½
1½
2½
3½
5-8
9-12
13+
AGE-GROUP

Figure 8. Ovulation rates of beaver in 11 NFCA habitats and the South-Saskatchewan.


MEAN NUMBER OF OVA
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
11
80
95
74
40
27
8
7
8
24
16
8
n
SD
$\bar{X}$
range
CL
(95%)
SS
P
Py
B
MH
Ch
ML
PA
Mo
C
F
UC
HABITAT

Ovulation rates were highest in the southern, high quality habitats and lowest in the low quality habitats of Cub, Foster and Uranium City.

Fetal Rates

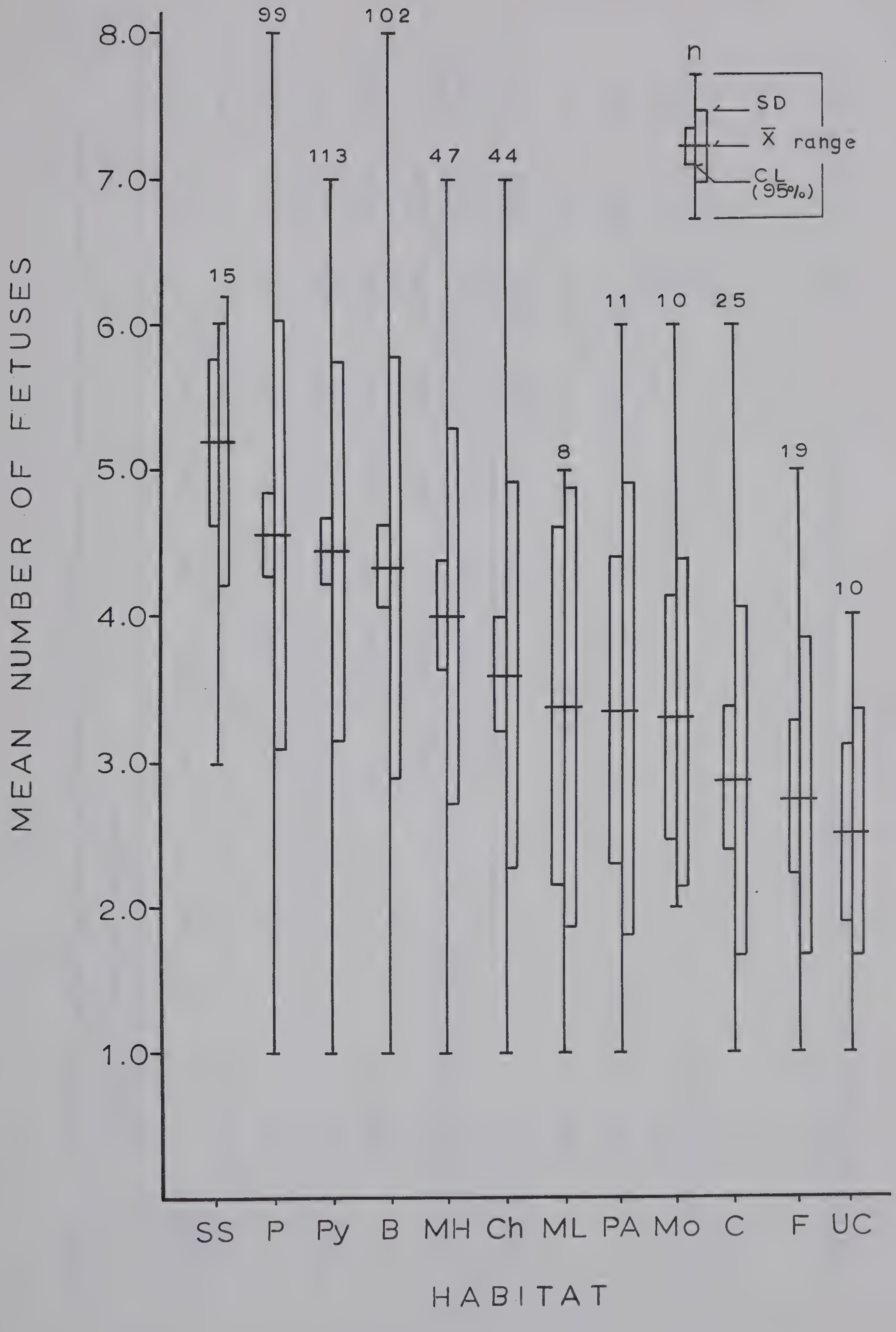
Four-year mean fetal rates ranged from 5.20 ± 0.56 in South-Saskatchewan to 2.50 ± 0.61 in the Uranium City habitat (Fig. 9 and Appendix III). Mean number of fetuses for all 503 counts was 4.09. The significance of the differences between mean fetal rates are provided in Table 7. Superimposing the harvest rating on Table 7 showed the following relationships: differences were highly significant between the high and low quality areas, and between the one moderate quality habitat and the low quality habitats; differences between the high and mediocre quality areas were significant; differences between high and high, mediocre and mediocre and low and low were not significant. The South-Saskatchewan had a mean fetal rate significantly greater than all other areas (difference between SS and P significant at 90 %).

Prenatal Mortality and Resorption Rates

There was no significant difference between the number of fetuses over 1 inch in length and those less than 1 inch in length ($P<0.9$). About two-thirds of all fetuses collected were over 1 inch in length. I, therefore, consider fetal rates to be good estimates of the number of young born. The difference between the number of corpora lutea and the number of viable fetuses is considered prenatal mortality.

Prenatal mortality ranged from 6.7 percent in Manitoba Lowland to 28.1 percent in Mostoos (Fig. 10). The highest losses in Prince Albert

Figure 9. Fetal rates of beaver in 11 NFCA habitats and the South-Saskatchewan.



MEAN NUMBER OF FETUSES
HABITAT
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
SS
P
Py
B
MH
Ch
ML
PA
Mo
C
F
UC
15
99
113
102
47
44
8
11
10
25
19
10
n
SD
$\bar{X}$
range
CL
(95%)

Table 7 P values* indicating the significance of the differences between means of fetal rates of beaver in various habitats

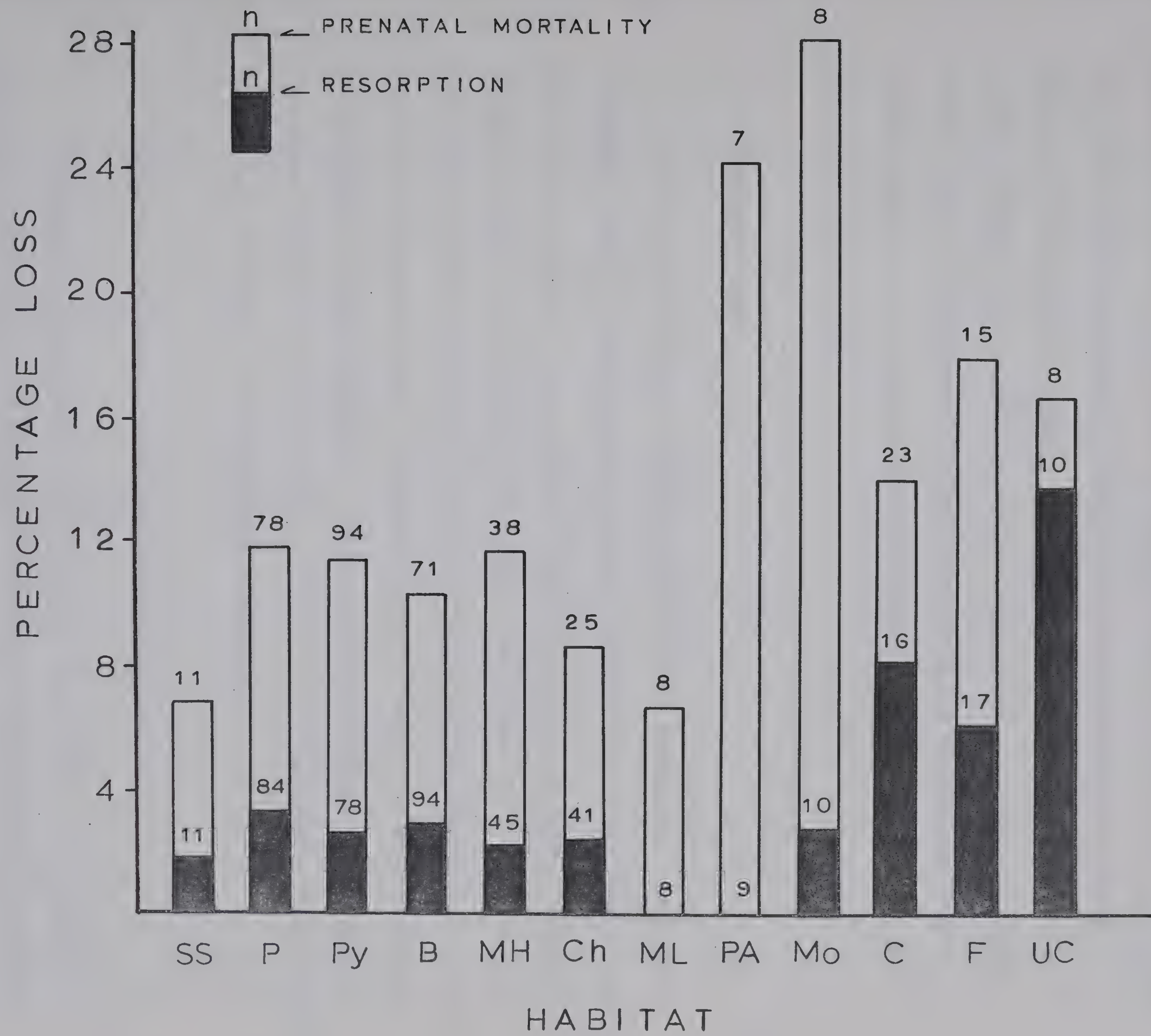
Quality Rating		SS	P	Py	B	MH	Ch	ML	PA	Mo	C	F	UC
	SS		0.1	0.01	0.01	0.001	0.001	0.01	0.01	0.001	0.001	0.001	0.001
High	P			0.5	0.3	0.05	0.001	0.05	0.02	0.01	0.001	0.001	0.001
	Py				0.7	0.1	0.001	0.1	0.05	0.01	0.001	0.001	0.001
	B					0.2	0.01	0.1	0.1	0.02	0.001	0.001	0.001
Moderate	MH						0.2	0.3	0.1	0.001	0.001	0.001	0.001
Mediocre	Ch							0.9	0.7	0.5	0.01	0.02	0.01
	ML								>0.9	>0.9	0.4	0.3	0.2
	PA									>0.9	0.4	0.3	0.2
	Mo										0.9	0.3	0.1
Low	C											0.7	0.3
	F												0.7
	UC												

* all values are < unless marked otherwise

Figure 10. Prenatal mortality and resorption rates of beaver in 11 NFCA habitats and the South-Saskatchewan.

Prenatal mortality was calculated from all beaver with complete corpora lutea and fetal counts: 1965 to 1968.

Resorption was calculated for all pregnant beaver during the 3 year period, 1966 to 1968.



n
PRENATAL MORTALITY
n
RESORPTION
PERCENTAGE LOSS
28
24
20
16
12
8
4
11
11
78
84
94
78
71
94
38
45
25
41
8
8
7
9
8
10
23
16
15
17
8
10
SS
P
Py
B
MH
Ch
ML
PA
Mo
C
F
UC
HABITAT

Uplands and Mostoos might be related to the small samples from those habitats. Mean prenatal mortality for each of the SS, high, moderate, mediocre and low quality habitat groupings were, respectively, 6.9, 11.3, 11.7, 14.0 and 15.8 percent. Thus, mean prenatal mortality varied inversely with habitat quality. Higher prenatal mortality in the low quality habitats was related to higher losses from resorption in those areas (Fig. 10). Resorption rates varied from 1.8 percent in South-Saskatchewan to 13.8 percent in the Uranium City habitat(excluding habitats of 0 resorption).

Pregnancy Rates

No pregnant kits were trapped in any habitat (Table 8). Calculated pregnancy rates of yearlings were probably higher than actual since trappers did not collect tracts from all immature animals trapped. Generally, pregnancy rates of 2-year olds were lower than those of adults. About two-thirds to three-quarters of the 2-year olds in the high quality habitats were producing young. Pregnancy rates of adults in most habitats were between 85 and 95 percent. The Uranium City habitat was an exception where the rate was 71.4 percent. There is some suggestion that female beaver over 12 years of age breed less frequently.

Variations in Reproductive Performance Between Years

While the differences in fetal rates in one habitat were generally not significant between years there were some trends suggested (Appendix III). The Bronson fetal rate remained remarkably steady. Between 1966 and 1968 fetal rates declined in the Churchill and Foster habitats. In

Table 8 Pregnancy rates (%) of beaver in South-Saskatchewan and 11 NFCA habitats

Habitat	½-1	1½-2*	2½-3	4-8	9-12	13+
South-Saskatchewan	0 (25)	0 (7)	100.0 (3)	88.9 (9)	100.0 (3)	
Pasquia	0 (11)	16.2 (37)	78.9 (20)	95.0 (60)	94.4 (18)	66.7 (6)
Porcupine	0 (14)	16.3 (49)	69.2 (15)	90.4 (83)	85.4 (21)	
Bronson	0 (78)	14.3 (42)	69.0 (36)	89.0 (64)	93.3 (15)	
Meadow Hills	0 (24)	30.4 (23)	38.9 (23)	91.3 (23)	100.0 (4)	50.0 (2)
Churchill	0 (6)	35.7 (14)	54.5 (11)	85.7 (21)	85.7 (7)	
Manitoba Lowland	0 (1)	0 (5)	50.0 (2)	100.0 (5)	100.0 (2)	
Prince Albert Uplands	0 (12)	6.3 (16)	20.0 (5)	85.7 (7)	100.0 (2)	100.0 (1)
Mostoos	0 (7)	36.4 (11)	0 (4)	100.0 (6)	100.0 (1)	
Cub	0 (13)	28.6 (7)		79.0 (19)	100.0 (8)	
Foster	0 (5)	16.7 (6)	66.7 (3)	93.3 (15)	100.0 (2)	
Uranium City	0 (1)	0 (1)	0 (1)	71.4 (14)		

* calculated yearling pregnancy rates are probably too high because trappers did not collect all non-pregnant yearling female tracts

Pasquia and Porcupine fetal rates were highest in 1966. Some trends in prenatal mortality were recorded (Appendix V). The Bronson rate declined yearly between 1965 and 1968; and the Churchill rate increased yearly during that period. Pregnancy rates appear to have remained relatively stable and high during the years of study (Appendix IV).

Relationship of Environmental Factors to Reproductive Performance

Latitude and Reproductive Performance

Comparisons of fetal rates between habitats in this study (Fig. 9) indicated a general decline with increases in latitude, but there were exceptions to that general rule. For example, the Churchill rate was greater than that in a number of more southern areas.

Fetal rates of beaver from various areas in North America (Table 9) suggest that there is an optimum latitude for high reproductive performance at least in the western states; and in western Canada and Alaska fetal rates declined with increases in latitude. There did not appear to be any correlation between latitude and fetal rates in eastern North America, but a much smaller range of latitudes was represented. Highest fetal rates were recorded in such widely separated areas as central Saskatchewan, central Alberta, Pennsylvania and Minnesota between latitudes 45° and 54° North.

Winter Diet and Reproductive Performance

The preferred foods of beaver are well known and require no reference support here. Aspen and balsam poplar, the two members of the preferred genus in central and northern Saskatchewan were readily avail-

Table 9 Fetal rates of beaver in various areas of its North American range: arranged in increasing latitude

Investigators	Area	Period	Number of Counts	Fetal Rate
Western North America				
Huey (1956)	New Mexico	1955	36	2.7
Grinnel et al. (1937)	California	1937	14	2.7
Rutherford (1964)	Colorado	1954-59	176	3.0
Osborn (1953)	Wyoming	1948	22	2.9
Leege and Williams (1967)	Idaho	1953-56	244	3.4
Leege and Williams (1967)	Idaho	1962-64	28	3.4
Provost (1958)	Washington	1951-56	115	3.6
Hammond (1943)	North Dakota	1942	18	4.2
Pearson and Flook (1958)*	PANP Sask	1954-58	24	3.5
Pearson and Flook (1958)	EINP Alberta	1958	8	6.3
(This study)	Saskatchewan	1965-68	503	4.1
Novakowski (1965)	northern Alta	1960-65	9	3.1
Hakala (1952)	Alaska	1951	11	2.8
Eastern North America				
Henry and Bookhout (1969)	Ohio	1966-67	16	4.8
Brenner (1964)	Pennsylvania	1959-62	24	5.5
Bond (1956)	Vermont	1950-56	58	4.1
Benson (1936)	Michigan	1935	21	3.9
Bradt (1938)	Michigan	1935	29	3.7
Longley and Moyle (1963)	Minnesota	1941-51	110	5.3
Hodgdon and Hunt (1955)**	Maine	1947-50	152	3.6

* includes placental scars, fetuses and young born to captive feaales
** includes some placental scars

able to beaver in the southern high quality habitats and in the South-Saskatchewan. Tallies of woody plants utilized in Porcupine and Bronson indicated that the poplars formed a very significant part of the diet of beaver in those areas. Litter sizes were highest in the high quality habitats.

Observations of foods utilized and stored in food caches in Cub, where the forests were primarily climax black spruce of 100 to 150 years of age or second-growth jackpine on burns, showed the use of white birch, willows, alders, jackpine and black spruce as well as the poplars. One food cache in Cub contained a large amount of labrador tea *Ledum groenlandicum*. I also observed beaver feeding on that shrub in Cub. During live-trapping in Foster during summer, 1967 tallies of beaver stumps suggested the most commonly used food was white birch. The utilization of rhizomes of water lilies *Nuphar variegatum* was commonly reported on collection labels by trappers in the more northern habitats where hardwoods are presumably restricted because of the long, cold subarctic climate. Reproductive performance was lowest in these low quality habitats.

Climate and Reproductive Performance

The following observations were noted when yearly reproductive performances were compared to climatic data (Table 10) for the four habitats with largest collections.

1. There was no correlation between reproductive performance and mean winter temperature. Neither the mild winter of 1967-68 or the cold winter of 1964-65 had any demonstrable effect on

Table 10 Climatic records and reproductive performance of beaver in four habitats

Habitat	Year*	Summer Rain (ins)	Snow (ins)	Mean Winter Temp.° F**	Ovulation Rate	Fetal Rate	Pregnancy Rate
Pasquia	1964-65	16.0	57.1	+ 5.9	4.77	4.33	100.0
	1965-66	17.7	68.1	+ 8.5	5.48	4.76	91.7
	1966-67	15.3	77.0	+ 6.2	5.30	4.50	95.8
	1967-68	7.8	90.7	+13.8	5.00	4.48	85.2
Porcupine	1964-65	16.0	57.1	+ 5.9	4.93	4.54	90.6
	1965-66	17.7	68.1	+ 8.5	5.25	4.71	92.6
	1966-67	15.3	77.0	+ 6.2	4.71	4.11	82.8
	1967-68	7.8	90.7	+13.8	4.44	4.15	93.8
Bronson	1964-65	11.5	35.0	+ 7.1	3.67+	4.44	100.0
	1965-66	15.8	37.7	+10.3	5.07	4.28	100.0
	1966-67	9.8	38.5	+ 9.0	4.71	4.34	87.1
	1967-68	7.0	60.3	+18.0	4.77	4.33	80.8
Meadow Hills	1964-65	11.5	35.0	+ 7.1	-	3.50	100.0
	1965-66	15.8	37.7	+10.3	4.75	4.10	88.9
	1966-67	9.8	38.5	+ 9.3	4.70	4.50	87.5
	1967=68	7.0	60.3	+18.0	3.86	3.64	90.0

* year starts in May
** for 6 month period November to April
\+ small sample
Snow=all snow during winter
-=no sample

reproductive performance.

2. In all four habitats the greatest ovulation rate followed the summer of greatest rainfall, but in only Pasquia and Porcupine did highest fetal rates follow that summer.
3. In both Pasquia and Meadow Hills lowest fetal rate followed the winter of least snow and lowest temperatures, but this relationship did not hold in the other two habitats.
4. Pregnancy rates were lowest following the summer of drought in both Pasquia and Bronson, but not in Porcupine and Meadow Hills.

Population Density and Reproductive Performance

Comparisons of reproductive performance and population density were made in the two habitats (Table 11) where numbers of beaver colonies per square mile were determined by the plot surveys and where reproductive tract collections were made. In both cases lower fetal rates were associated with denser populations. The differences in fetal rates were not significant but trends were suggested.

Comparisons of fetal rates with colony size (Table 12) showed that the observed mean number of fetuses was lower in larger colonies in Cub and Porcupine but differences were not significant. In Porcupine both females in the pair colonies were young beaver, 2½ and 3½ years of age; and were therefore expected to produce somewhat smaller litters (see Fig. 11). This might have masked the effect of smaller colony size in the latter area.

Table 11 Beaver density and fetal rate (Mean ± 95% CL)

Year	Churchill		Foster	
	Density*	Fetal Rate	Density	Fetal Rate
1965-66	0.80	3.90 ± 0.92	0.59	3.50 ± 0.92
1966-67	0.83	3.68 ± 0.57	0.65	2.57 ± 1.50
1967-68	0.98	3.00 ± 0.94	0.66	2.83 ± 1.40

* colonies per square mile

Table 12 Colony size and fetal rate (n in parenthesis)

Beaver per Colony	Fetal Rate	
	Cub	Porcupine
2	3.00 (4)	3.50 (2)*
3-5	2.67 (9)	
6-10	2.50 (2)	3.40 (5)

* both females were young (see text)

Age and Reproductive Performance

Comparison of age and fetal rate of beaver of the Porcupine habitat (Fig. 11) indicated that females between the ages of 5 and 8 years averaged the greatest number of fetuses. Yearlings, breeding for the first time, and females over 10 years of age had the smallest numbers of fetuses. The Porcupine was selected for this comparison because it was the area of largest samples.

In the Pasquia in 1967 one 14-year old beaver had three fetuses and a 16- or 17-year old had only one, after having resorbed a fetus. In 1968 in the same habitat, a 19-year old was the only barren individual in a collection of 15 beaver. The ovaries of that 19-year old contained four regressing corpora lutea of ovulation.

The relative importance of various age-groups to the breeding portion of each population is shown in Table 13. Actual breeder proportions represent the percentage of total pregnant animals in each age-group collected in one habitat. Potential breeders are all females minus kits. Potential breeder proportions were taken from age ratio data on the basis of a 1:1 sex ratio.

Yearling proportions of actual breeders were low in both the high and low quality habitats. Such proportions were highest in the Meadow Hills, Churchill and Mostoos habitats. This suggests that yearlings were breeding more frequently in, at least, some of the moderate and mediocre habitats than in either high or low quality habitats. In addition, yearlings were considerably less available in the low quality habitats compared to the high quality habitats. This further suggests that yearlings may have been breeding more frequently in relation to

Figure 11. Age-specific fetal rates of the Porcupine beaver: 1965 to 1968 data combined.

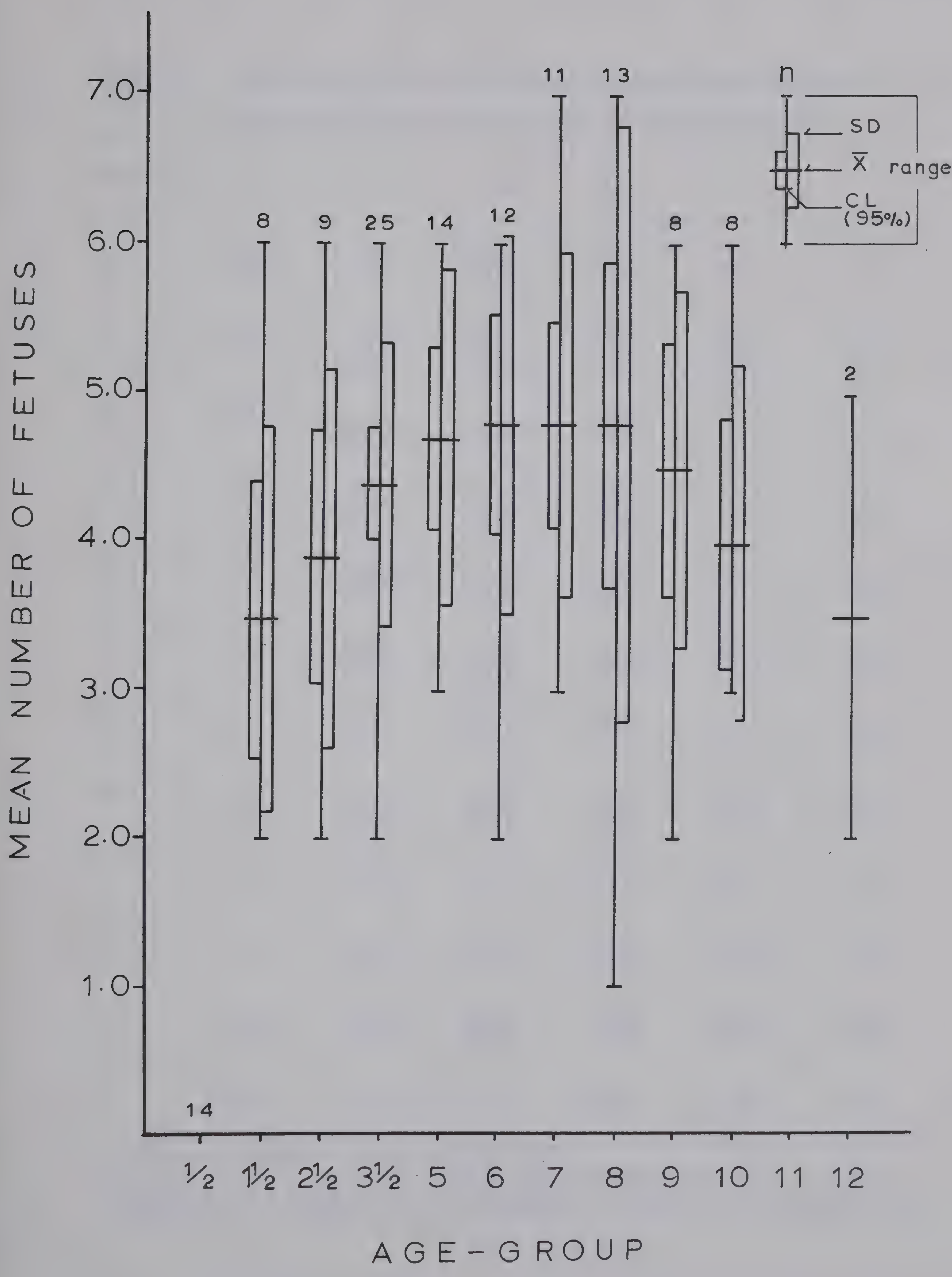

MEAN NUMBER OF FETUSES
7.0
6.0
5.0
4.0
3.0
2.0
1.0
14
8
9
25
14
12
11
13
8
8
2
n
SD
$\overline{X}$ range
CL (95%)
½ 1½ 2½ 3½ 5 6 7 8 9 10 11 12
AGE-GROUP

Table 13 Comparisons of actual female breeder proportions to potential breeder proportions in various habitats

Habitat		1½	2½	4-8	9-12	13+
SS	13*	0	15.4	61.6	23.1	0
P	99	6.1** / 49.9	15.2 / 16.3	57.5 / 21.0	17.2 / 10.1	4.0 / 2.7
Py	110	7.3 / 44.5	8.2 / 12.5	68.2 / 31.3	16.4 / 9.0	0 / 2.7
B	96	6.3 / 37.0	20.8 / 20.8	59.4 / 36.2	13.4 / 4.9	0 / 1.3
MH	40	17.5 / 38.5	17.5 / 23.8	52.5 / 29.0	10.0 / 5.6	2.5 / 3.1
Ch	35	14.3 / 37.0	17.1 / 16.1	51.4 / 38.2	17.1 / 6.1	0 / 2.5
ML	8	0	12.5	62.5	25.0	0
PA	11	9.1 / 38.6	9.1 / 22.9	54.6 / 31.4	18.2 / 5.8	9.1 / 1.3
Mo	10	40.0	0	50.0	10.0	0
C	25	8.0 / 30.7	0 / 21.7	60.0 / 33.7	32.0 / 9.9	0 / 4.1
F	19	5.3 / 24.3	10.5 / 18.1	73.7 / 47.1	10.5 / 8.2	0 / 2.5
UC	10	0	0	100.0	0	0

* number of pregnant animals collected

** $\frac{\text{actual}}{\text{potential}} = \frac{\text{proportion of all pregnant animals}}{\text{proportion of potential breeders (all females-kits)}}$

their availability in low quality areas than in high quality areas.

Two-year olds formed between 0 and 20.8 percent of breeders in various habitats; and were breeding in about equal proportion to their availability in most habitats.

In all habitats over 50 percent of the females with fetuses were between the ages of 4 and 8 years, even though these animals formed relatively low proportions of potential breeders. There is a suggestion that these animals formed somewhat lower proportions of actual breeders in relation to their availability in the low quality habitats.

Animals over 12 years of age formed small proportions of total breeders.

Body Weight and Reproductive Performance

Body weights (Fig. 7) and fetal rates (Fig. 9) were both significantly greater in Porcupine than in Cub.

In Cub fetal rate increased with increasing body weight (Table 14). Differences between the means were not significant, but regrouping and comparing fetal rates of those beaver with body weights of 45.0 pounds and over with those of 40.0 pounds and less gave a significant difference ($P<0.05$). Age did not seem to introduce a bias.

Minimum Breeding Age

As indicated in Table 13 yearlings were breeding and producing young in most habitats. On March 8, 1965 a pregnant 6-year old female was removed from colony 1 on the intensive study area. The adult male was not captured; and on March 22 a yearling female was trapped. She was an

Table 14 Body weights and fetal rates of Cub beaver

Weight Range	n	Fetuses $\overline{x}$	Fetuses range	Ages
30.1 - 35.0	3	2.33	2-3	5,6,8
35.1 - 40.0	4	2.50	2-3	5,6,10,12
40.1 - 45.0	5	2.60	1-4	6,7,9,10,12
45.1 - 50.0	3	3.67	3-5	4,8,10

unusually large animal for a yearling, with a body weight of 36 pounds. The uterus had enlarged and appeared to be preparing for implantation. No corpora lutea were noted. The yearling had not been captured during the October live-trapping although two others were (Fig. 6).

Periods of Conception and Birth

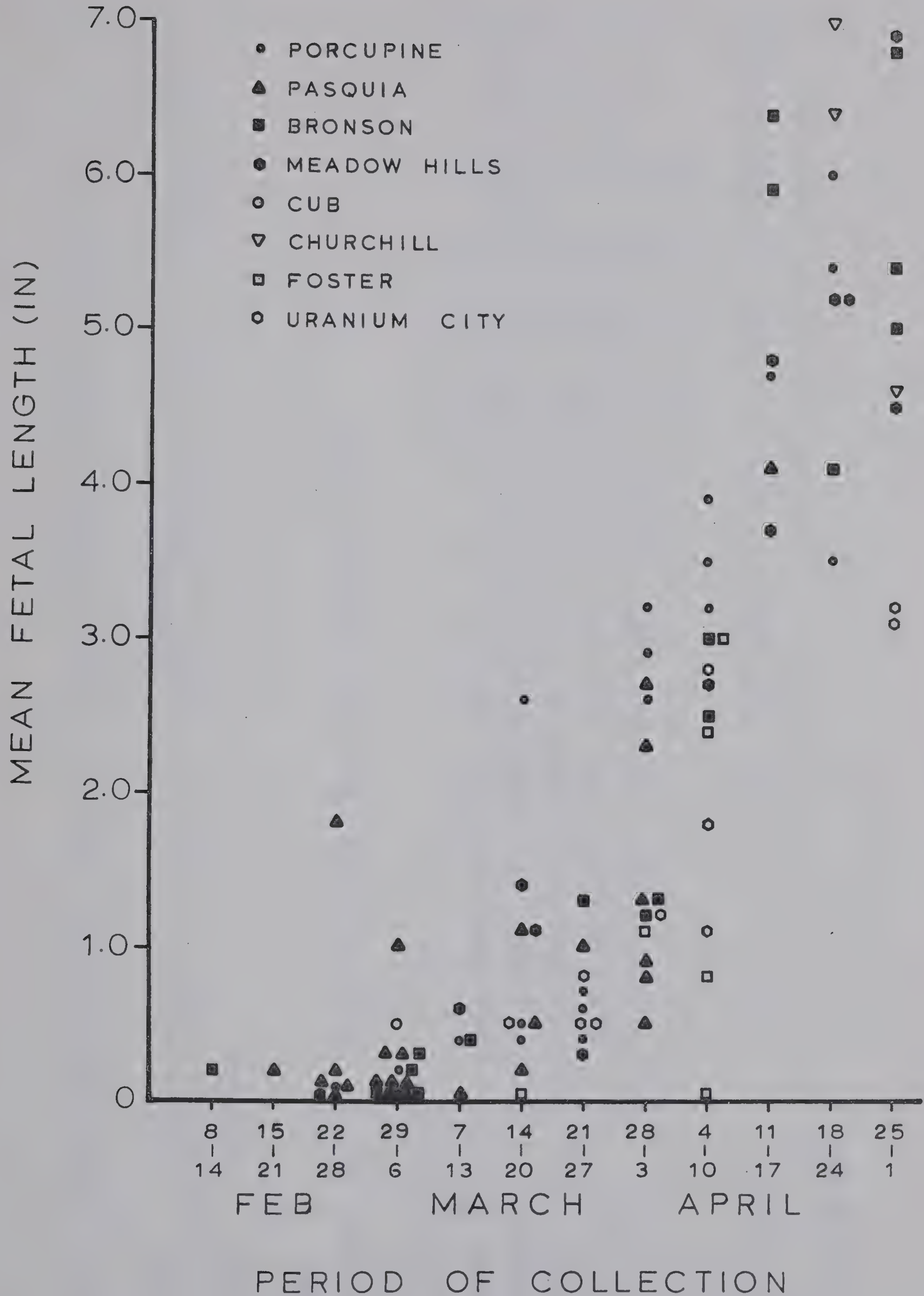
Comparisons of fetal development between habitats (Fig. 12) suggest that conception and time of birth occur later in northern habitats than in southern habitats. Assuming a period of about 2 weeks post-ovulation before fetuses are visible most breeding appears to take place about mid-February and most births about mid-May in the southern habitats. The wide range of fetus size during most collection periods indicate a corresponding wide range of conception time in both the southern and northern habitats. First occurrences of visible fetuses in southern habitats indicate that some beaver breed in late January and others as late as mid-March.

Sex Ratios

Fetal sex ratio, 50.5 percent males, was about balanced (Table 15). Few cases of resorption were found in fetuses large enough to be sexed. Fetal sex ratio is therefore considered an accurate measure of secondary sex ratio. During summer live-trapping a slight excess of males was found in animals in their first 2 years of life, but adult females outnumbered adult males in the trapped sample during the summer and fall periods.

At 22 colonies live-trapped both adults were captured at nine col-

Figure 12. Scatter diagram of mean fetal lengths from eight habitats in 1968. Habitats are listed from south to north.



PORCUPINE
PASQUIA
BRONSON
MEADOW HILLS
CUB
CHURCHILL
FOSTER
URANIUM CITY
MEAN FETAL LENGTH (IN)
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
8-14
15-21
22-28
29-6
7-13
14-20
21-27
28-3
4-10
11-17
18-24
25-1
FEB
MARCH
APRIL
PERIOD OF COLLECTION

Table 15 Fetal, summer and winter sex ratios of beaver in various habitats (% males)

Habitat	Age-group							
	Fetal	½-1	1½-2	2½-3	3½-4	5-8	9-12	13+
Grouped	50.5 (390)							
Summer								
(C,Py,B,F)		53.6 (28)	57.9 (19)	85.7 (7)	34.8 (23)*			
Winter								
Pasquia		57.5 (120)	50.0 (82)	63.6 (22)	36.4 (11)	48.0 (25)	40.0 (20)	33.3 (3)
Porcupine		54.9 (184)	52.2 (69)	56.5 (23)	38.5 (26)	34.3 (35)	47.4 (19)	100.0 (4)
Bronson		57.4 (101)	54.5 (55)	62.5 (24)	44.4 (27)	45.8 (24)	16.7 (6)	0:1 (1)
Meadow Hills		62.0 (50)	46.7 (30)	35.7 (14)	70.0 (10)	33.3 (12)	42.9 (7)	66.7 (3)
Cub		59.3 (86)	46.0 (50)	56.7 (30)	55.6 (27)	47.7 (44)	45.8 (24)	77.7 (9)
Foster					50.0 (8)	50.0 (20)	40.0 (5)	
Total (winter)		57.3 (541)	50.3 (286)	56.6 (113)	47.8 (109)	43.8 (160)	42.0 (81)	70.0 (20)

* adults grouped

onies. There did not seem to be any particular order of capture indicated at these nine colonies; at four of the colonies both adults were captured the same day. However, at the remaining 13 colonies where one adult was taken, it was a female 11 times. These data suggest that the adult male may have been absent from some of the summer colonies. The alternative explanation is a trap-selection for the adult female.

Kill-trapping records showed more kit males trapped than females. When the data were classed according to the habitat groupings (page 35) kit males significantly outnumbered kit females ($P<0.05$). An analysis of the order of capture of kits in kill-trapping on both the intensive study area and the Peter Burym trapline showed that there was no bias towards either sex. Males were caught first 13 times and females 14 times.

Sex ratio of kill-trapped yearlings was 1:1, and that of 2-year olds was slightly biased towards males although the difference was not significant.

In adult beaver from 3½-4 to 12 years females were more often trapped than males. Grouping the data showed a significant difference at the 80 percent level. An analysis of the order of capture of kill-trapped adults on the two areas showed that females were more often trapped first. At 26 colonies where both adults were trapped the adult female was trapped before the adult male 18 times. This difference is significant at the 80 percent level. This suggests a trap-selection for the adult female and may explain the biased adult sex ratios. This would result in an excess of adult males at some point in the population; and in fact, more males 13 years of age and older were taken in the harvest ($P<0.2$). In addition, on the two study traplines at five colonies where both of the adults were 10 years of age or over the combined age of the males out-

numbered the females by 5 years (Table 6).

Age Structure

Approximately 5, 10 and 10 percent of all beaver trapped in the NFCA were collected and aged during 1965-66, 1966-67 and 1967-68, respectively. In most habitats the same trappers were collecting each year and a variety of trapline locations were involved. With the exception of the Foster trappers, those trappers who participated appear to have collected mandibles from virtually all the beaver they trapped. Samples of the harvest should be representative of the harvest as a whole.

In Saskatchewan trappers are permitted to place traps or snares in lodge entrances. Generally the trapper makes an effort to locate all entrances and to block or insert a trap in each one. The first beaver passing through is caught. This method was used in kill-trapping colonies on the intensive study area and the Peter Burym trapline. An analysis of the order of capture by age (Table 16) showed that kits, yearlings and adults were caught first in about equal proportion to their availability. From these data I conclude that there is no age bias in kill-trapping. Age structures of beaver in harvests are judged to be good estimates of actual population age structures.

Variations of Age Structure Between Habitats

The proportions of kits in the harvest varied from a high of 51.5 percent in Pasquia to 23.4 percent in Foster when age structure over the 3 year period was averaged (Fig. 13). Yearling proportions ranged from 24.3 percent in Churchill to 18.6 percent in Foster. Two-year olds varied

Table 16 Order of capture of kill-trapped beaver in 21 family-group colonies in the intensive study area and the Peter Burym trapline

Age-group	Order of Capture										Totals
	1	2	3	4	5	6	7	8	9	10	
Kits	10	8	11	13	6	4	3	2	0	1	58
Yearlings	4	4	2	4	2	1	2	0	2	0	21
Adults	7	9	8	1	4	2	1	0	0	0	32
Totals	21	21	21	18	12	7	6	2	2	1	111

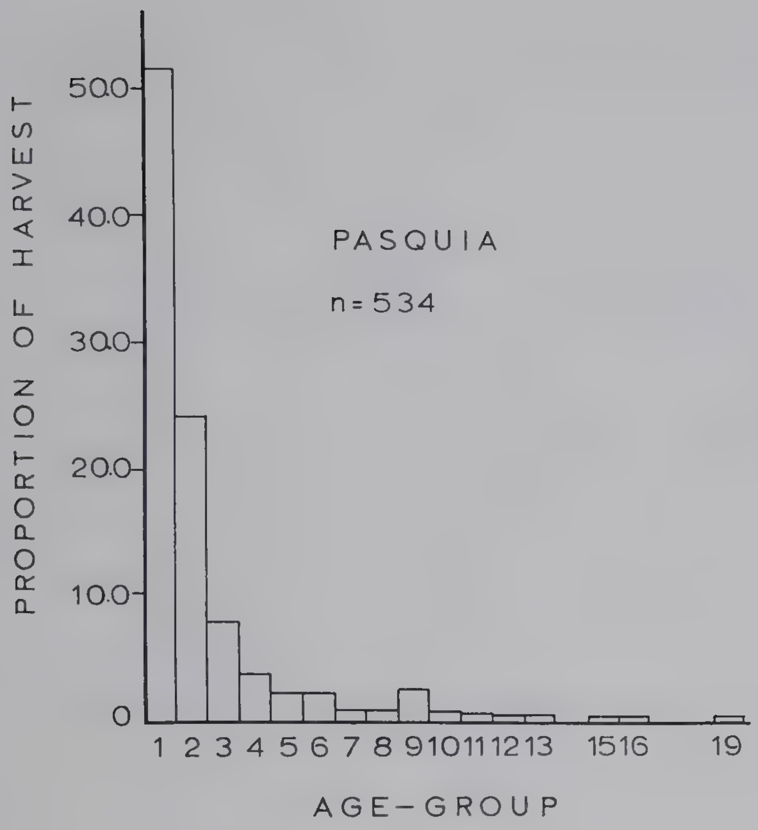
Figure 13. Age structures of the beaver harvest in eight NFCA habitats: 1965-66, 1966-67 and 1967-68 harvests combined. The Foster data were adjusted (see Methods).

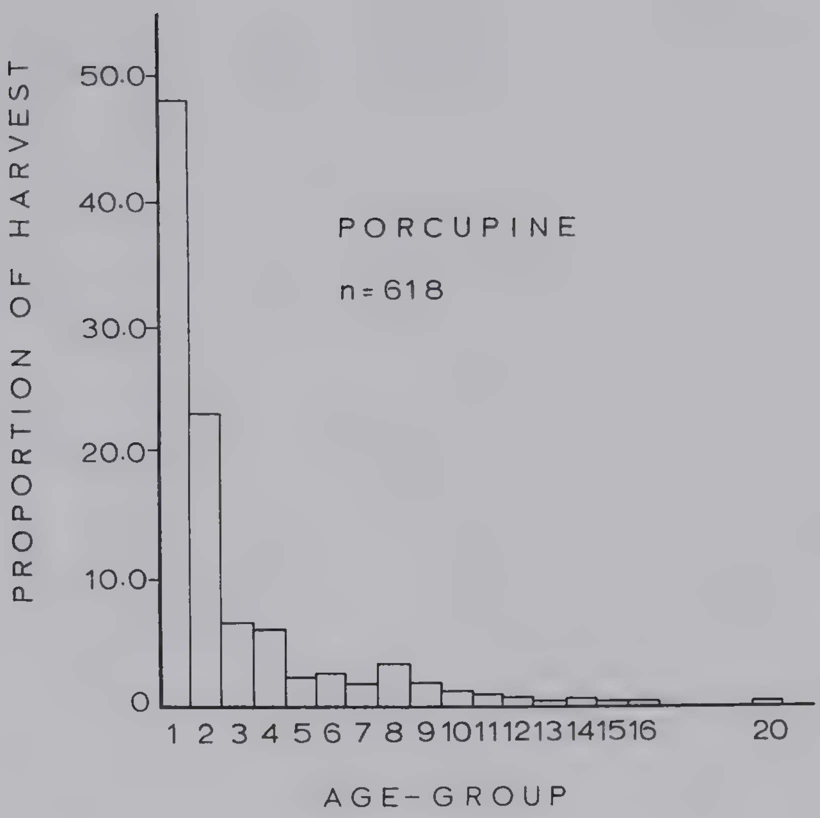
1 = ½-1

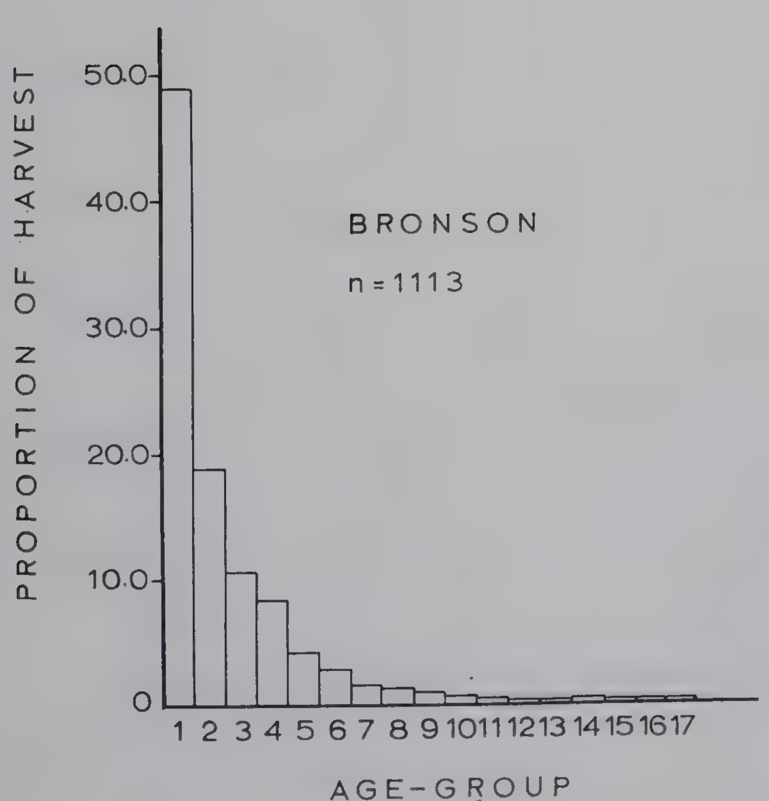
2 = 1½-2

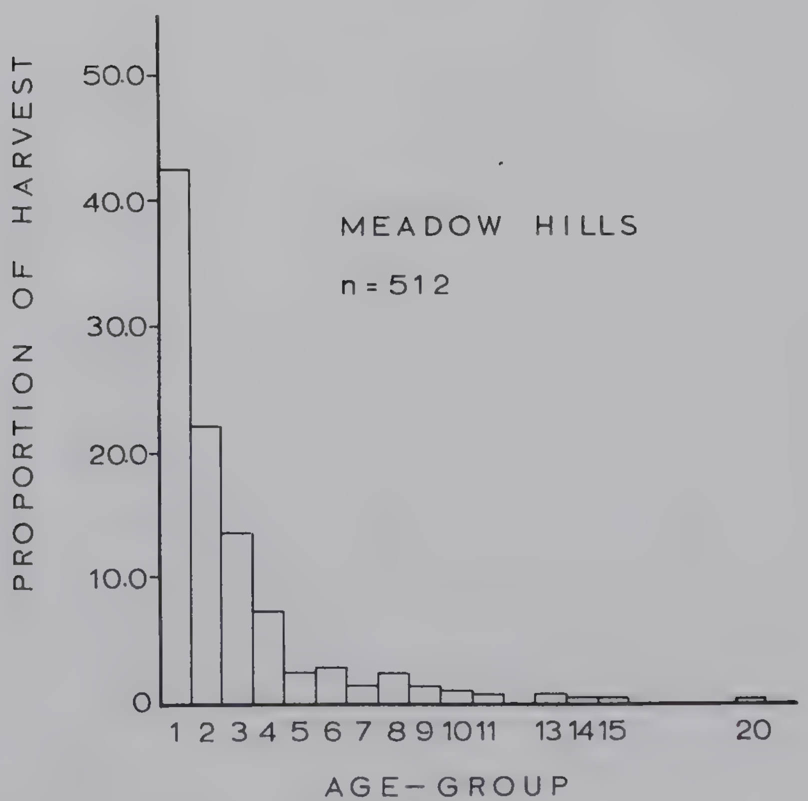
etc.

13a

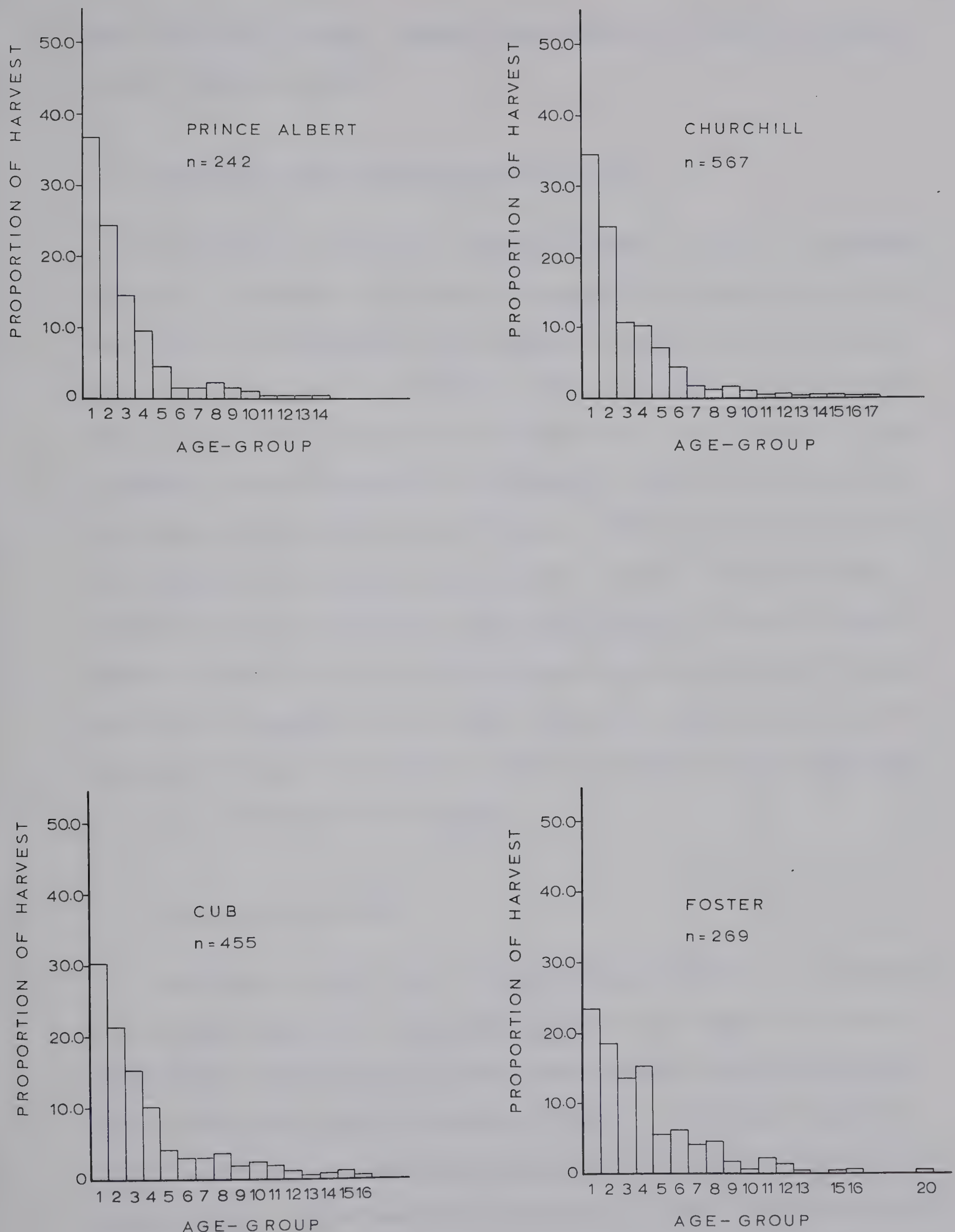

PROPORTION OF HARVEST
50.0
40.0
30.0
20.0
10.0
0
PASQUIA
n=534
1 2 3 4 5 6 7 8 9 10 11 12 13 15 16 19
AGE-GROUP


PROPORTION OF HARVEST
50.0
40.0
30.0
20.0
10.0
0
PORCUPINE
n=618
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 20
AGE-GROUP


PROPORTION OF HARVEST
50.0
40.0
30.0
20.0
10.0
0
BRONSON
n=1113
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
AGE-GROUP


PROPORTION OF HARVEST
50.0
40.0
30.0
20.0
10.0
0
MEADOW HILLS
n=512
1 2 3 4 5 6 7 8 9 10 11 13 14 15 20
AGE-GROUP

13b


PROPORTION OF HARVEST
PRINCE ALBERT
n = 242
AGE-GROUP
CHURCHILL
n = 567
CUB
n = 455
FOSTER
n = 269

from 6.5 to 15.2 percent. Adults varied from 16.3 percent in Pasquia to 34.2 percent in Foster.

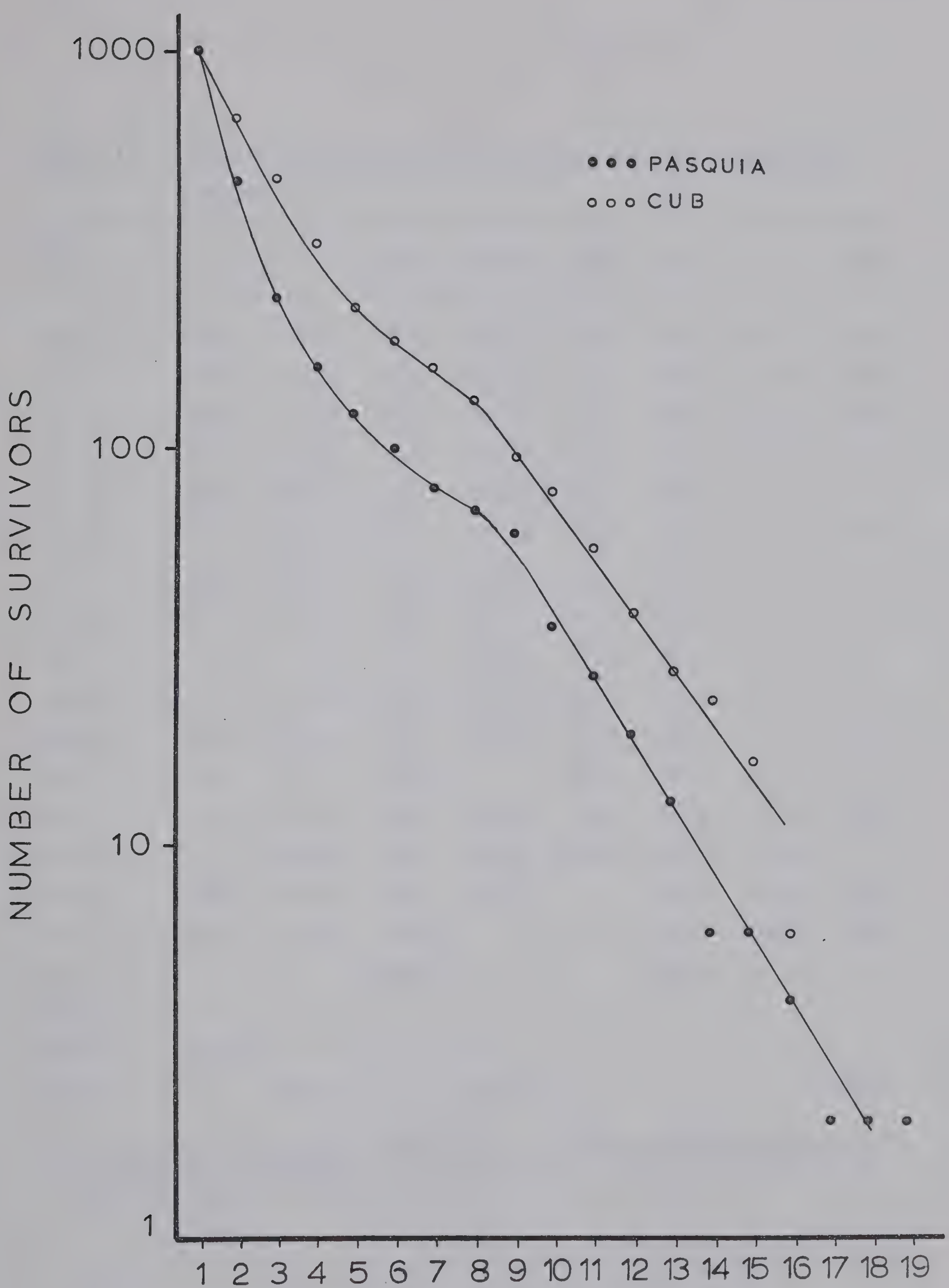
Variations of Age Structure Between Years

The raw data on which this section is based are shown in Appendices VII to IX. In Bronson, the habitat from which the largest collections were made, the proportion of kits remained relatively stable, varying only between 45.3 and 53.1 percent. This corresponded with the stable yearly fetal rates (Appendix III) of that area. The proportion of kits in 1965-66 and the proportion of yearlings in 1966-67 were low in both the Pasquia and Manitoba Lowland habitats. The fetal rate in Pasquia in 1965 (Appendix III) was the lowest of the 4 years. In the Manitoba Lowland the low kit proportions 1965-66 followed by 1 year the trapper reports of beaver mortality and corresponded with the decline in population size as suggested by the census (Fig. 5). The following year the kit proportion was 60.8 percent. This was the year of rapid population increase as reported by the trappers.

Survival and Mortality

Survivorship curves (Fig. 14) using Pasquia and Cub as representatives of high quality and low quality habitats, and cumulative mortality rates (Table 17) of beaver in eight habitats were calculated using the Dynamic Life Table method of Eberhardt (1969). This method assumes a stable population, a requirement that was not met in all habitats in the current study. Populations were increasing, at least in the Meadow Hills and Churchill areas, with a modest increase suggested for Foster (Fig. 5

Figure 14. Survivorship curves of the Pasquia and Cub populations: 1965-66 to 1967-68 data combined. Curve locations estimated.



PASQUIA
CUB
1000
100
10
1
NUMBER OF SURVIVORS
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
AGE-GROUP

Table 17 Cumulative mortality rates of beaver in eight NFCA habitats

Age-group	P	Py	B	MH*	PA	Ch*	C	F*
½- 1	51.5	48.1	48.9	42.6	36.8	34.4	30.1	23.4
1- 2	75.7	71.4	67.7	64.6	61.2	58.7	51.6	42.0
2- 3	83.5	77.8	78.3	78.3	75.7	69.8	66.8	55.8
3- 4	87.3	84.0	86.7	85.7	85.5	79.7	76.9	71.0
4- 5	89.5	86.2	90.8	88.3	90.1	86.9	80.9	76.6
5- 6	91.9	88.8	93.7	91.2	91.7	91.4	83.7	82.9
6- 7	92.9	90.6	95.3	92.8	93.4	93.3	86.6	87.0
7- 8	93.8	94.0	96.9	95.1	95.5	94.5	90.3	91.8
8- 9	96.4	96.0	97.8	96.5	97.1	96.3	92.1	93.7
9-10	97.4	97.1	98.7	97.5	98.3	97.4	94.3	94.4
10-11	98.1	98.1	99.3	98.2	98.8	97.7	96.0	96.7
11-12	98.7	98.7	99.4		99.2	98.4	97.1	98.1
12-13	99.4	99.0	99.5	99.0	99.6	98.6	97.6	98.5
13-14		99.5	99.7	99.4	100.0	99.1	98.2	
14-15	99.6	99.7	99.8	99.8		99.6	99.3	98.8
15-16	99.8	99.8	99.9			99.8	100.0	99.5
16-17			100.0			100.0		
17-18								
18-19	100.0							
19-20		100.0		100.0				100.0

* populations estimated to be increasing - calculated mortality rates may not be valid

and Table 3).

Calculations of mortality by this method also do not include mortality of kits during that period prior to the trapping season. The only estimate of mortality during that period is the 2.7 percent calculated at ten colonies in the intensive study area. This bias will be discussed.

The survivorship curves indicate that mortality was highest in both areas during the first 2 or 3 years of life and somewhat lower in the adult age-groups from about 5 to 9 years and high again in old age. Cumulative mortality rates (Table 17) indicate that population turnover is much faster in the high harvest habitats. Mortality during the first year of life in Pasquia was double that of the Foster beaver. Mortality after 6 years of life in Cub and Foster was equal to mortality in Pasquia after only 3 years of life. By the time beaver reach the age of 10 years in the southern high quality habitats only three of an original 100 survive, and only five or six in any of the habitats.

Observations of Mortality From Causes Other than Trapping

Every spring during or soon after break-up there are sporadic reports of dead beaver. In spring, 1965, however, trappers from a number of areas especially in and around the Manitoba Lowland habitat, reported finding many dead beaver. Game Management Officer, F. W. Terry conducted a preliminary survey in the Beaver Lake area in June and found an additional nine dead animals. Carcasses were too far decomposed for examination and none were submitted for autopsy. In July I accompanied Terry on another survey. We did not find any dead beaver, but we did collect six beaver by trapping. Subsequent autopsy by the Saskatchewan Department

of Agriculture in Regina indicated these beaver contained no known pathogens.

Remains of two dead kits, that might have been killed by predators, were found on the intensive study area. A mandible, a portion of the vertebrae, and some hair were found in the snow during the spring melt near colony 3-62. Position of the remains in the snow indicated a winter death. The other, found at a colony in the northern part of the study area after the spring melt, appeared to have died the preceding fall judging by its dental development. Only the mandible of that beaver remained. Lynx *Lynx canadensis* scats were associated with the latter remains.

Occasional examination of wolf *Canis lupus* scats in the field showed that beaver were being utilized by wolves on the study area.

Trapping Intensity

First year rates of recovery of tagged beaver in the Porcupine, Bronson and Foster habitats were 29.2, 50.0 and 0 percent, respectively (Table 18). First year recovery rates in Cub varied from 8.0 to 40.9 percent and second year rates from 10.8 to 16.0 percent. Third year rates were 8.0 and 8.1 percent and the one fourth year rate was 2.7 percent. Even though trappers in the intensive study area were directed to colonies with tagged beaver, only 45.9 percent of the animals tagged in 1964 were subsequently trapped in the 4 succeeding years of harvest. Since trappers in the intensive study area were directed to specific colonies, calculated recovery rates are probably biased upwards and do not represent a measure of trapping intensity for the habitat as a whole.

Table 18 Tag recovery rates of beaver in four NFCA habitats

Habitat	Year Tagged	n	Year Recovered								Total	
			1		2		3		4			
			n	%	n	%	n	%	n	%	n	%
Cub	1964	37	9	24.3	4**	10.8	3	8.1	1	2.7	17	45.9
Cub	1965	25*	2	8.0	4	16.0	2	8.0			8	32.0
Cub	1966	22*	9	40.9	3	13.6					12	54.5
Cub (Mean)				24.4		13.5		8.1				44.0
Porcupine	1967	24	7	29.2								
Bronson	1967	16	8	50.0								
Foster	1967	9	0	0								

* does not include tagged beaver from previous year or years recaptured in 1965 and 1966

** includes two beaver captured outside of study area

DISCUSSION

The Effect of Harvest on Population Change

The large harvests of the late 1950's and early 1960's, the subsequent declines in harvest and the increase in population size following years of low harvests suggested that trapping had been a factor limiting beaver population growth. This seemed to be especially true in at least the large Churchill and Hyper-Churchill habitats where populations were increasing rapidly between 1965 and 1967 (Table 3). I believe that the increases in numbers of beaver in these two habitats can be directly related to the closure of a number of Conservation Areas to beaver trapping in 1963-64 and the low quotas in subsequent years.

Other investigators have commented on the effects of trapping on beaver populations. Longley and Moyle (1963) reviewed the history of the "Beaver Trade" in North America and along with others (Johnson 1927, Swank 1949) pointed out that extermination of beaver from the eastern United States in the 1700's and 1800's was a result of the intensive quest for beaver by trappers. Fuller (1953) reported beaver populations were reduced in the Fort Providence area of the Mackenzie District by a combination of destructive forest fires and heavy trapping pressure. Pozzo and Stephenson (1963) remarked that beaver populations on Michipicoten Island in Lake Superior were kept low in the 1920's and 1930's by poachers. Restrictions on trapping are generally credited for the return of beaver to most North American areas following the hey-days of the Fur Trade.

The Regulation of Beaver Numbers in Colonies

Although only two habitats were sampled adequately, there seemed to be sufficient evidence indicating that greater numbers of beaver were maintained at colonies in higher quality habitats. Observations in this study that supported the above suggestion were the greater numbers of beaver at colonies in Porcupine versus Cub including more kits, yearlings and 2-year olds at family-group colonies, and the dispersal of yearling animals from parental colonies in the low quality habitat of Cub. I suggest that the greater number of beaver at colonies in Porcupine reflected the greater availability and quality of the food resources, that carrying capacities of colony-sites were greater in Porcupine than in Cub, and that the beaver adjusted their numbers accordingly. The chief mechanism of that regulation were variations in mean litter size between the two areas and the apparent greater frequency of dispersal of immature animals from parental colonies in the low quality areas.

The dispersal of yearlings from parental colonies in their second summer of life is not a well known phenomenon. Since Bradt (1947) showed convincing evidence for the dispersal of 2-year olds in their third summer of life, it has been generally accepted that beaver remain for at least 2 complete years at the parental colony. There have been, however, observations made by other investigators that support my contention that yearling dispersal occurs and that it is important as a method of regulation of beaver numbers at colonies.

Semyonoff (1951) working with beaver introduced into unoccupied habitats in the Soviet Union, found that beaver did in fact leave parental colonies during their second summer of life. He further pointed out

that it was in areas of lower-quality habitats that this emigration continued for the longest time. In Michigan, Bradt (1938) intensively trapped one colony of beaver over a period of 6 years. For 3 consecutive years in a row the number of beaver at the colony was maintained at 12. This was accomplished by variations in the number of young born earh year and by the number of immatures dispersing from the colony. In one year when six kits were born, six immatures left the colony. Four of these were 2-year olds and two were yearlings. My analysis of the data of Townsend (1953) and Leege (1968) showed that some yearlings emigrated from parental colonies in their second summer of life in both areas. Neither investigator related the emigration to habitat type.

That this regulation is related to food availability or quality of the habitat is supported by the observations of Rutherford (1964). He trapped to "extirpation" colonies in two habitats. He found a mean of 5.1 beaver in colonies in aspen areas and a mean of 4.5 in willow areas.

Habitat Quality and Types of Colonies

It was shown that single-occupant and pair colonies were mainly occupied by yearlings and 2-year olds (Table 6). Thus, given a greater tendency to dispersal of immature animals in low quality habitats there should be more single-occupant and pair colonies in such areas. This, however, was not the case (Table 4). An alternative explanation is that more intensive trapping in high quality habitats fragments family-groups and results in more single-occupant and pair colonies. Direct support for this idea comes from the observations of colonies in Porcupine a month or so after the kill-trapping had terminated. Single-occupant colonies

were common during that period (Table 4). Bradt (1947), Patric and Webb (1953) and Hodgdon and Hunt (1955) all reported single-occupant and pair colonies.

The Regulation of Reproduction

The suggestion, in this study, of a direct relationship between litter size and the proportion of preferred foods in the diet, is supported by observations of other investigators. In Colorado, Yeager and Rutherford (1957) and Rutherford (1964) have related habitat and diet to fetal rate. In cottonwood-willow habitats of less than 5,000 feet elevation the mean fetal rate of 40 beaver was 4.4; in aspen-willow habitats between 6,000 and 8,000 feet the mean fetal rate of 87 females was 2.7; and 49 females averaged 2.3 fetuses in aspen-willow habitats over 8,000 feet. These workers concluded that "less rigorous winters, greater availability, and presumably higher food quality at the lower elevations are reflected in higher productivity."

In New Mexico, Huey (1956) found a relationship between kinds of food and number of young produced by beaver. He found an average of 2.06 fetuses per female where willow was the principal food; 2.74 in cottonwood areas; and 4.20 in aspen areas. Longley and Moyle (1963:31) in Minnesota stated, "it seems likely that much of the high productivity reflects good food supplies, especially aspen."

The variations in prenatal mortality (page 55) suggested that the effect of diet on reproduction is not totally at ovulation. In Colorado, Rutherford (1964) also found that prenatal mortality varied between habitats. He recorded 9 percent loss in high quality habitats at low elev-

ations, 13 percent loss in medium elevation habitats and 25 percent in poor habitats above 8,000 feet.

All of these results support the theory that reproduction of beaver varies directly with quality of habitat, particularly with availability and presumably quality of the preferred foods. Similar relationships have been suggested in studies of other mammals. Cheatum and Severinghaus (1950) in New York found ovulation and fetal rates of white-tailed deer *Odocoileus virginianus* highest in habitats they considered to be of highest quality, as did Taber and Dasmann (1958) for *Odocoileus hemionus columbianus* in California. Edwards and Ritcey (1958) thought that high twinning rates of some moose *Alces alces* in British Columbia were a result of higher quality pastures at higher elevations. Pimlott (1959) found a higher twinning rate of moose in Newfoundland in an area where the vegetation was of high nutritional value than in an area of lower quality. Going one step further, Verme (1969) in studies of penned white-tailed deer found a greater fawning rate in deer on high energy diets.

The direct relationships of increasing latitude and litter size, as shown in some mammals by Lord (1960), was not found to hold for beaver in Saskatchewan or in North America as a whole. For a review of supporting and opposing evidence to Lord's hypothesis the reader is referred to Sadleir (1969a).

The inverse relationship between litter size and both number of beaver in colonies (Table 12) and colony density (Table 11) suggests a density-dependent mechanism. There is little evidence from other beaver studies that either support or oppose this finding. Pearson and Flook (1958) compared litter sizes of beaver in Prince Albert and Elk Island National Parks (Table 9). In PANP they observed small litters in a dense

population with a mean of 8.2 beaver per colony. The habitat in PANP was over-utilized and a density-dependent control mechanism was postulated.

Sadleir's (1969a) review of density and reproduction indicated a varying relationship between litter size and stage of population cycle in microtine rodents, quoted a number of observations of inverse density-dependency in non-cyclic species and noted Errington's (1963) findings of direct density-dependency in the muskrat. It is probably safe to conclude that reproductive density-dependency has been demonstrated for many species and is normally inverse in relationship as was suggested for beaver in this study.

The lack of relationship between mean winter temperature and litter size (Table 10) is worthy of further examination. The observations made at colony 2-63 (page 47) where both reproductive performance and body weights were maintained during at least 2 months of critical conditions provide evidence that beaver are able to adapt successfully for long periods to situations of low environmental temperature without the excessive loss of body energy reserves. Novakowski (1967) recorded what he considered to be extremely reduced activity of beaver during winter in colonies he studied in northern Alberta. He reasoned that beaver made use of colonial behavioral traits such as huddling which reduced energy losses during periods of low temperature. The small burrows and lack of activity at 2-63 suggest the beaver huddled for much of the 2-month period.

Aleksiuk and Cowan (1969a), from measurements of body weight, fat reserves and thyroid activity, have postulated a low level of metabolic activity in beaver of the Mackenzie Delta, NWT, during winter. Further

to that, in laboratory experiments, they (1969b) demonstrated a decline in food intake and activity of northern beaver under decreasing light conditions. This was not found with southern beaver. They suggested, therefore, that an inherent mechanism of adaptation to periods of low energy availability existed in northern beaver.

If extra energy had to be used to maintain body temperatures during long, cold winters insufficient energy for the production and growth of fetuses might result. Such a situation could conceivably cause higher prenatal mortality. This apparently did not happen in the Saskatchewan beaver during the cold winter of 1964-65. All of these results suggest that winter temperature has little influence on reproductive performance of beaver.

The fact that ovulation rate was highest in all four areas following the summer of greatest rainfall, and that pregnancy rate declined somewhat in two of the habitats following the drought year, suggests that reproduciive performance of beaver might depend, in part, on water levels. Increased rainfall could have had an indirect influence on reproduction through the production of extra growth of food plants of perhaps higher nutritional value. It may be significant that pregnancy rate was lowest in 1968 in Bronson. Of the four habitats examined, this habitat is probably most susceptible to water losses during drought years because of its southwestern location and its sandy soils.

The relationship between age and litter size (Fig. 11) has been observed in other mammals such as white-tailed deer (Eberhardt 1960) and moose (Simkin 1965).

Since body weights and fetal rates were both significantly greater in Porcupine than in Cub, I believe that both body weight and reproduct-

ive performance of beaver are influenced by the quality of the habitat as suggested by Rutherford (1964). Gill (1956) found that size of deer and the fawn:doe ratio were both highest in certain habitats and lowest in other habitats in West Virginia.

Other investigators have found that litter size varies with body weight. Both Poole (1960) and Lloyd (1963) found ovulation rate varied directly with body weight of *Oryctolagus cuniculus*, and Kalela (1957) found highest fetal rates in *Clethrionomys rufocanus* in animals of largest body weight. Litter size of beaver of the intensive study area also appeared to vary directly with body weight. It seems apparent that body weight has a definite influence on reproduction of the above species; and that body weight, in turn, is dependent on habitat quality and probably heredity.

The Breeding of Yearling Beaver

Bailey (1927) concluded that beaver may breed at 1½ years, and Osborn (1953) found 21.2 percent of "sub-adults" (his weight data suggest that these were primarily yearlings) were pregnant in Wyoming. Benson (1936), Bradt (1947) and Brenner (1964) all claimed a minimum breeding age of 2½ years. Provost (1958:44) found, "that most female beaver in Washington are not physiologically capable of breeding until they reach a body weight of between 30 and 35 pounds." He concluded that most female beaver do not begin breeding until the third season following their birth, but that some probably do breed in their second year. Provost further remarked, "that a good deal of the discrepancy among various authors concerning the minimum breeding age of beaver probably stems from

a lack of uniform and accurate criteria for determining age in these animals." Methods commonly used before 1964 depended on such characters as body weight and pelt size.

Following the development of the dental aging technique more accurate estimates of minimum breeding age have been made. Larson and van Nostrand (1968) showed that some beaver in Maryland and Nova Scotia were sexually mature at 1½ years of age. Henry and Bookhout (1969) also found a minimum breeding age of 1½ years for Ohio female beaver. The results of these recent studies are similar to those of this study.

Analysis of yearling breeding is probably not simple. Provost's suggestion that a certain body weight must be reached before initial breeding can successfully occur has support from Sadleir (1969b). Provost's 30 to 35 pound requirement for successful initial breeding would appear to hold for the Saskatchewan range. Most yearlings in the low quality habitats have not reached that weight range (Fig. 7). This probably explains the low incidence of yearling reproduction in those areas (Table 13). Most yearlings in the high quality habitats have reached that weight range (Fig. 7), but yearling reproduction was, nevertheless, still not common. If I am correct in assuming that yearling dispersal occurs less frequently in high quality habitats, then the presence of a dominant adult breeder at the parental colony could discourage yearling reproduction. Out of hundreds of colonies checked, only two pregnant animals were found in each of two colonies.

This social pressure acting against yearling reproduction might not have been as effective in some of the moderate and mediocre habitats, such as Meadow Hills and Churchill, where rapidly expanding populations and high yearling breeding were indicated.

In some areas trappers take only a portion of the beaver present at a colony. The observation of apparent yearling selection by the adult male following the loss of the adult female (page 66) could explain some yearling female reproduction.

Productivity

Kit proportions of the population at harvest time are used in this study as an estimate of productivity.

There is a general belief among trappers that primarily large animals will be captured if traps are placed a considerable distance from the lodge. In many North American areas trappers employ that method and others to ensure that as few kits as possible are caught. This is so because kit pelts are worth much less than those of larger beaver. In such areas or where regulations require trappers to place traps a certain distance from the lodge, harvests may not be representative of the population.

In Alaska, Buckley and Libby (1955) thought that age structures from harvest collections were not representative of the true population age structure, but they attributed this to the fact that trappers were retaining young beaver for their own use and were marketing only the large animals because of the much greater value of their pelts. Larson (1967) assumed a trap bias existed, but he did not indicate in which direction the bias would act. Leege and Williams (1967) assumed age ratios in the harvest in Idaho equalled population age ratios. In Ohio Henry and Bookhout (1969) used age structures to calculate juvenile mortality. They assumed ratios in the harvest equalled population ratios.

Since there were no restrictions on trap placement in Saskatchewan during the study period and no particular age was selected in the harvest (page 72) kit proportions in harvests are considered unbiased measures of productivity.

The high kit proportions in all three of the high quality habitats indicated populations of very high productivity. This reflected the reproductive performance of the beaver of those areas. High productivity was probably maintained by the removal of large portions of the population each year in commercial trapping operations.

The somewhat lower productivity of the beaver of the moderate and mediocre habitats and the much reduced productivity of the beaver of the low quality habitats reflected the lower reproductive performance of the beaver of those areas.

The age composition of Maryland beaver from 1962 to 1966 was 27.3 percent kits, 17.5 percent yearlings, 24.4 percent 2-year olds and 30.8 percent adults (Larson 1967). Populations of seemingly low productivity were also found in Idaho by Leege and Williams (1967). In that study kit proportions varied from 20 percent in commercial harvests to 24 percent in summer and fall live-trapping.

The composition of an Ohio population in 1966-67 was 41.6 percent kits, 16.4 percent yearlings, 9.6 percent 2-year olds and 32.4 percent adults (Henry and Bookhout 1969). The productivity of that population ressembles that of the Meadow Hills beaver in this study.

Earlier estimates of productivity may not be as reliable because less reliable aging techniques were used. Hodgdon and Hunt (1955) in Maine, using pelt measurements as an indicator of age, found 37 percent kits, 16 percent yearlings and 47 percent 2-year olds and adults. These

proportions apparently agreed very closely with estimates made from colony observations. A population of moderate productivity is indicated. Longley and Moyle (1963) estimated ages from skinned carcass weights and reported 37.7 percent adults, 36.8 percent yearlings and 25.6 percent kits. The low proportion of kits in the harvest suggests low productivity, but this does not agree with the high reproductive performance of the Minnesota beaver of that period (Table 9). Measurements of reproduction were probably better estimates of productivity than age structure in that area because of the aging technique used.

These studies suggest that the beaver of the Pasquia, Porcupine and Bronson habitats had as high a productivity as has been recorded for beaver. The level of productivity in those areas during the study period may have approached the upper limit of productivity of a beaver population.

The Sources of Mortality

Trapping

Trapping was obviously a major mortality agent in most habitats during the study period. The recovery data from the intensive study area must be considered inconclusive for reasons already given. However, the recovery of only 45.9 percent of the 1964 tagged animals does suggest that other sources of mortality are important in that area. The importance of mortality from trapping in the southern, high quality habitats was demonstrated at least in the high 1-year recovery in Bronson. More work is required to more completely quantify trapping mortality.

Predation

Since predation on beaver by wolves in this study was not measured, its importance can only be estimated. Beaver remains occurred in 7 percent of 420 scats in the Rocky Mountain National Parks of Canada, but 17 percent of the summer scats collected in that study contained beaver remains (Cowan 1947). Nash (1951) reported observations of wolves stalking beaver in northern Manitoba and the occurrence of beaver hair in wolf scats. He concluded that the wolf was an important predator of beaver in that area. Beaver constituted the second most important wolf food on Isle Royale, Lake Superior where they occurred in 10 percent of 438 scats (Mech 1966). In Ontario, Pimlott (1967) found beaver represented 7 percent of the food items in 1,435 scats and were the third most common food item of wolves in Algonquin Park. In one area of Ontario, Pakesley, beaver were the most important food and were present in 59 percent of 206 scats collected (Pimlott, Shannon and Kolenosky 1969).

All of the above observations with the possible exception of Cowan were made in habitats similar to that found in northern Saskatchewan where one or two ungulate species are the most important food of wolves. While no direct evidence of wolves killing beaver were observed in the Saskatchewan studies, it should be noted that I did not specifically set out to record such information. It would be naive not to include the wolf as an important predator of beaver in areas where wolves and beaver are common.

Wolf populations were almost non-existant in Bronson and Porcupine during the study period and were reduced in Pasquia and Meadow Hills by continual wolf poisoning programs. In all other habitats the wolf was common throughout the study period despite wolf poisoning. Wolves

probably did not control beaver numbers in any habitat, but where trapping was not intensive, losses to wolves might have been significant.

Other potential predators of beaver in northern Saskatchewan besides the wolf are the coyote *Canis latrans*, black bear *Ursus americanus*, lynx, otter *Lutra canadensis* and woverine *Gulo luscus*. Attempts by black bears to dig into colonies were fairly common in northern Saskatchewan. Other investigators have suggested that the bear is attracted by the wimpering of new-born kits and attempts to dig such litters out (Swank 1949, Nash 1951). Semyonoff (1951) reported observations of other Soviet investigators of bear, lynx and otter predation on beaver. Saunders (1963) found beaver remains in lynx scats in Newfoundland; and Packard (1940) reported coyote predation on beaver. The wolverine may occasionally take beaver. This mustelid has been so reduced by trapping and poisoning in Saskatchewan that it now occurs only sparingly in the very northern parts of the northern forest. These five predators undoubtedly do take some beaver in the northern forest, but numbers taken are probably low compared to losses to wolves. However, they do contribute to mortality from predation.

Disease

Beaver die-offs are well-known phenomena and have been reported from most of the beaver's range. Such die-offs were especially common in the 1940's and 1950's in North America (Jellison, Kohls, Butler and Weaver 1942, Stenlund 1952, Ruttan 1953, Banfield 1954 and Rutherford 1964). Connell (1956) reviewed the results of examinations of beaver specimens collected from Manitoba, Saskatchewan and Alberta during the early 1950's. His summary indicated the presence of *Pasteurella tularensis* and *P.*

pseudotuberculosis in the beaver of the three prairie provinces. Tularemia was also isolated from animals in Ontario, Minnesota and Colorado.

The only die-off reported in the northern forest during the study period occurred in the Manitoba Lowland habitat and surrounding area in 1964-65. Losses from disease were therefore not common during the study period and disease is judged a minor mortality agent.

Others

Pelts from the first year's harvest on Michipicoten Island, Lake Superior were so heavily scarred that fur buyers were reluctant to bid on them. Pozzo and Stephenson (1963) attributed the scars to intraspecific strife in that population, believed to be the densest ever recorded. While scarring of pelts was occasionally noted in Saskatchewan harvests, fighting was probably not an important mortality agent during the period of study.

Some deaths due to starvation, old age, accidents and perhaps exposure and parasitism must occur.

Variations in Survival and Mortality

The high survival of beaver during the first summer as found in this study has been noted elsewhere. Rutherford (1964:10) writing of first year mortality of beaver in Colorado, stated "certainly some postnatal and juvenile mortality occurs, but it is believed that this will rarely exceed 10 percent of the total number of young born." Bradt (1947) found low mortality of beaver during the first summer of life. He noted that the mean number of kits live-trapped per colony in the fall was practically

equal to the mean number of fetuses observed in uteri. These results suggest that survival of beaver during the first few months of life is very high.

In this study calculations of mortality did not include losses of kits during the first few months of life. Subsequent comparisons of mortality between habitats would be biased if kit survival varied. Since trapping is not conducted during the summer and there did not seem to be any other major mortality agents besides predation, predation is probably the only mortality agent that might have varied significantly between habitats during the summer period. Results on the intensive study area where the wolf population was substantial and kit survival high suggest that predation on such young animals is not common. Young beaver remain in the lodge for about a month after birth, do not stray far from the lodge during the first summer and apparently do not go on land until fall (Hodgdon and Hunt 1955). This suggests that predation on kits during the summer is uncommon. First summer losses of beaver may be minor in habitats with and without wolves. Comparisons of mortality between habitats where populations were stable should be valid.

Habitat and Mortality

Differences in survival (Fig. 14) between the high quality and low quality habitats are primarily due to higher losses of young beaver in the former areas. This higher mortality in the high quality habitats seems to be related to more intensive trapping (Table 18) in such areas. Less intensive trapping in the more northerly habitats must have allowed greater losses to more abundant predators and to other mortality agents.

Age-Specific Mortality

The differences in age-specific mortality (Fig. 14) must be a result of other mortality agents if there is no age bias in the harvest. Studies of natural mortality of other long-lived mammals have generally indicated that mortality rates are highest in the very youngest and oldest animals. Fuller (1962), Mech (1966), Pimlott et al. (1969) and Hornocker (1970) all found that large predators selected ungulates that were either very young or old (Fuller 's data included a third group of various-aged bison which he called the "handicapped"). Houston (1968) found that these same age-groups of moose (i.e., very young and old) were most susceptible to winter losses even where predation was not an important mortality agent.

Age-specific mortality of beaver as found in this study ressembled that of ungulate mortality of the above studies, except that higher losses appeared to continue into the second and third year of life of the beaver. Beaver mortality in the second and third years of life might be related to the dispersals of yearlings and 2-year olds during those periods. These animals are probably more susceptible to losses from predation and perhaps exposure and fighting in other established beaver territories through which they must travel. The higher rates of loss during the years of life after 10 years probably reflect more deaths due to accidents, old age and predation.

Sex-specific Mortality

Sex ratios found in commercial harvests in this study were similar to those found previously by other investigators (Table 19). Unfortunately, very few studies to date have accurately determined sex ratios at

Table 19 Sex ratios of beaver in trappers' harvests (% males)

Investigator	Fetal	Kits	Yearlings	Adults
Benson (1936)*		54.3		39.3
Bradt (1938)**	52.2			
Osborn (1953)***	56.3	57.1		46.8
Hodgdon and Hunt (1955)		51.3	56.9	48.4
Bond (1956)+			54.5	45.7
Rutherford (1964)***		53.6	41.2	50.0
Leege and Williams (1967)++		61.7	58.0	47.1
(This study)	50.5	57.3	50.3	45.9

* yearlings and 2-year olds included with adults
** newly-born kits less than 2 months of age
*** 2-year olds included with adults
\+ yearlings (between 21 and 30 pounds): adults (over 30 pounds)
\++ total of two trapping periods; fall and spring

birth and few investigators compared sex ratios from harvest collections to independently determined ratios in live populations. Results of Bradt's studies and this study suggest that sex ratio at birth is very nearly balanced. Since virtually all investigators have reported more kit males than females in harvests there must be either more female mortality during the first year of life or a trap selection for kit males. Since my analysis of the order of capture of kits on the two study traplines indicated there was no bias, I tentatively conclude that natural mortality of kit females does exceed that of kit males.

Most investigators have not attempted to explain the reasons for more adult females in harvests. Others (Osborn 1953, Leege and Williams 1967) quoted Grinnell et al. (1937) who thought that there was a higher natural mortality of males due to fighting during the breeding season. Since the entire breeding season in Saskatchewan occurs during winter when the male is restricted to one colony under ice, I doubt that this explanation has much merit, at least in the northern distribution of the species. Bond (1956) reasoned that some genetic factor may be responsible for the loss of males.

There was a strong suggestion in this study that adult females are more susceptible in the harvest than males of that age. Since adult females were not all that more common in harvests than males it may be that the trap-selection mortality of females is nearly balanced by higher natural mortality of adult males. Males apparently undertake extensive summer travels while the females remain at the parental colony-site to rear young (Hodgdon and Hunt 1955, Longley and Moyle 1963). Losses during travel in strange surroundings are probably in excess of those in the familiar territory of the colony-site. These studies indicate that

more intensive investigations are required to more accurately evaluate sex-specific mortality and its significance to the population.

Beaver and Trapping in Low Quality Habitats

The trapping system employed on the intensive study area was based on the assumption that a) the adult pair would produce a litter each year, b) dispersal of 2-year olds would take place in the fourth summer of occupation and c) the harvest during the fourth winter would remove all the remaining family-group. The 2-year olds would then start a new family and the rotation (a harvest every 3 years is a 3-year rotation) would continue.

The low harvest at kill-trapped colonies that were left for 4 years indicated that such a long term trapping system was impractical in that area. I believe that the reasons for this are as follows:

1. Before the 4-year period was up the food supply had been depleted and the beaver had moved. Annual movements of family-groups to new food supplies occurred. Some new family-groups moved into the area (Fig. 6, colony 1 and 30) and some tagged families disappeared and presumably moved out of the area.
2. The number of animals at colonies was low because of emigration of yearlings as well as 2-year olds, and small litters. The high rate of yearling dispersal had the effect of creating colonies of one and two beaver throughout the area as well as reducing the number of beaver in parental colonies. This process lowers the mean number of beaver per colony and distorts estimates of population size.

3. It seems logical that greater frequency of movements of both family-groups and dispersing immatures would increase the chances of losses from predation. Animals in the familiar territory of their own colony must have a survival advantage.
4. Density operated to lower reproductive performance as colony size increased. Evidence from at least two colonies suggested that kits were not produced every year.
5. Trappers were unable to remove all the beaver at parental colonies during the spring trapping. Earlier trapping would increase the chances of taking more of the beaver.

Shorter term rotations and earlier harvests are needed in such low quality habitats. The 3-year rotation might have worked better in a high quality area.

CONCLUDING DISCUSSION AND RECOMMENDATIONS

I have made the suggestion that intensive trapping during the late 1950's and early 1960's was responsible for the reduction in population size and harvests, at least in some habitats, such as Churchill and Hyper-Churchill. Evidence for a decline in numbers of beaver is largely based on the reduced harvest trend and is, therefore, primarily circumstantial. Checks of the trappers' census during that period were few in number but suggested that trappers were reluctant to report fewer colonies. The combination of an over-estimated population and an increasing number of trappers resulted in larger harvests from smaller populations. More intensive management is required. The numbers of trappers should be carefully regulated and the number of beaver more accurately determined.

Judging from the results of census checks during the study period the trappers' census is a fairly imprecise measure of population size over large areas. Management requires a census from each trapline in order to establish individual beaver quotas. The census is and should continue to be the basic tool of beaver mangement. However, an alternative method of determining trends in population size in the northern forest is required. For this reason I recommend that the plot method, developed during the study period, be utilized. Permanent plots should be established and surveyed each fall. This would provide trends in numbers of colonies and a more accurate and continuing record of population size.

Observations of the numbers and ages of beaver in colonies in two habitats strongly suggested that colonies in high quality habitats contained more beaver than colonies in low quality habitats. Higher harvests are in order in the higher quality areas.

Rotational systems of harvest, based on trapping colonies every other year or every 3 years, have the advantage of distributing trapping more uniformly over the entire trapline and allow production at untrapped colonies. In some areas, trappers who do not employ such methods, retrap a colony each year until it has been trapped out. The results of the rotational harvest method on the intensive study area suggested that short term rotations would be advisable in low quality habitats. Losses from yearling dispersal, family-group movements and lower reproduction would be minimized.

Further investigation is recommended in the following areas:

1. Variations of immature dispersal between habitats of varying quality should be more accurately quantified. Results of this study suggested that the frequency of immature dispersal varied and was important in regulating the numbers of beaver at colonies. In addition, the question of whether immatures are forced from the colony or leave voluntarily has apparently not been resolved. This could be the subject of further research.
2. Food utilization studies of wolves in other areas have suggested that the beaver is an important prey species. Greater movements of beaver in low quality habitats probably increases their susceptibility to predation which may replace trapping as the most important mortality agent in areas where trapping is not intensive. Further investigation of wolf-beaver relationships in the northern forest is recommended.
3, Natural mortality during the dispersal and pre-mating phase of life and its effect on sex and age ratios in the population has not been intensively studied. Further work is suggested.

4. This study suggested that a density-dependent mechanism operated to lower litter size in larger populations. The data are few, and the implications must, at best, be considered tentative. This relationship, if correct, basically means that more intensive trapping can result in increasing reproductive performance of survivors. Additional research is suggested.
5. That there is a selection for adult females in Saskatchewan and possibly other harvests throughout the North American range was suggested in this study. Selection of the mature female could prove to be limiting under certain conditions. Further investigation should include independent determinations of the sex ratios in the population and in the harvest.

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Appendix I Mean winter temperatures (°F)* and precipitation levels (inches) at recording stations in or near major beaver habitats

Habitat	Recording Station	1964 Rain	1964-65 Snow	1964-65 Mean Winter Temp	1965 Rain	1965-66 Snow	1965-66 Mean Winter Temp	1966 Rain	1966-67 Snow	1966-67 Mean Winter Temp	1967 Rain	1967-68 Snow	1967-68 Mean Winter Temp
Pasquia Porcupine	Hudson Bay	16.0	57.1	+5.9	17.7	68.1	+ 8.5	15.3	77.0	+6.2	7.8	90.7	+13.8
Bronson Meadow Hills	Loon Lake	11.5	35.0	+7.1	15.8	37.7	+10.3	9.8	38.5	+9.0	7.0	60.3	+18.0
PA Uplands	Prince Albert	8.2	41.1	+6.0	10.7	40.9	+ 6.9	11.9	53.1	+7.0	6.1	40.3	+15.3
Cub Churchill	La Ronge			+4.6	13.7	64.0	+ 5.3	12.0	51.7	+3.8	10.2	81.2	+12.0
Foster	Foster Lake				11.5	83.8		9.1	66.8		10.3	60.7	
Uranium City	UC	8.7	47.7	-2.2	11.0	65.0	- 0.1	11.9	100.8	-3.9	6.3	104.8	+ 5.7

* for 6 month period November to April

Appendix II Ovulation rates of Saskatchewan beaver

Habitat	1965	1966	1967	1968	SE	Mean ± 95% CL
South-Saskatchewan	5.00 (2)*	5.00 (3)	5.50 (66)		0.273	5.27 ± 0.61 (11)
Pasquia	4.77 (13)	5.48 (21)	5.30 (20)	5.00 (26)	0.155	5.10 ± 0.31 (80)
Porcupine	4.93 (27)	5.25 (24)	4.71 (28)	4.44 (16)	0.136	4.86 ± 0.27 (95)
Bronson	3.67 (3)*	5.07 (14)	4.71 (35)	4.77 (22)	0.156	4.76 ± 0.31 (74)
Meadow Hills		4.75 (16)	4.70 (10)	3.86 (14)	0.202	4.43 ± 0.41 (40)
Churchill	4.00 (1)	4.30 (10)	4.00 (14)	4.00 (2)	0.294	4.11 ± 0.61 (27)
Manitoba Lowland		4.14 (7)		2.00 (1)	0.441	3.86 ± 1.04 (8)
PA Uplands		5.00 (2)	4.40 (5)		0.469	4.57 ± 1.15 (7)
Mostoos Upland		4.00 (4)		4.00 (4)	0.423	4.00 ± 1.00 (8)
Cub	3.33 (9)	3.27 (11)	2.50 (2)	3.50 (2)	0.296	3.25 ± 0.61 (24)
Foster	2.00 (3)	3.75 (4)	3.50 (4)	3.40 (5)	0.323	3.25 ± 0.69 (16)
Uranium City				3.00 (8)	0.267	3.00 ± 0.63 (8)
Total						4.56 (398)

* small samples account for ovulation rates less than fetal rates: sample size not normally equal because ovaries were incomplete or missing on some tracts

Appendix III Fetal rates of Saskatchewan beaver

Habitat	1965	1966	1967	1968	SE	Mean ± 95% CL
South-Saskatchewan	5.74 (4)*	5.00 (5)	5.00 (6)		0.262	5.20 ± 0.56 (15)
Pasquia	4.33 (15)	4.76 (29)	4.50 (26)	4.48 (29)	0.147	4.55 ± 0.29 (99)
Porcupine	4.54 (35)	4.71 (31)	4.11 (27)	4.15 (20)	0.122	4.42 ± 0.24 (113)
Bronson	4.44 (8)	4.28 (29)	4.34 (38)	4.33 (27)	0.144	4.32 ± 0.29 (102)
Meadow Hills	3.50 (3)	4.10 (19)	4.50 (12)	3.64 (14)	0.187	4.00 ± 0.38 (47)
Churchill	3.00 (3)	3.90 (10)	3.68 (25)	3.00 (6)	0.199	3.59 ± 0.40 (44)
Manitoba Lowland		3.71 (7)		1.00 (1)	0.533	3.38 ± 1.26 (8)
PA Uplands	2.00 (2)	3.74 (4)	3.60 (5)		0.476	3.36 ± 1.06 (11)
Mostoos Upland		3.40 (5)		3.20 (5)	0.386	3.30 ± 0.87 (10)
Cub	3.00 (9)	2.70 (10)	2.75 (4)	3.50 (2)	0.242	2.88 ± 0.50 (25)
Foster	1.50 (2)	3.50 (4)	2.60 (7)	2.83 (6)	0.252	2.74 ± 0.53 (19)
Uranium City				2.50 (10)	0.269	2.50 ± 0.61 (10)
Total						4.09 (503)

* number of tracts with fetuses in parenthesis

Appendix IV Pregnancy rates of adult Saskatchewan beaver

Habitat	1965	1966	1967	1968	Mean
South-Saskatchewan	100.0 (1)*	100.0 (5)	83.3 (6)		92.3 (12)
Pasquia	100.0 (11)	91.7 (24)	95.8 (24)	88.0 (25)	92.9 (84)
Porcupine	90.6 (32)	92.6 (27)	82.8 (29)	93.8 (16)	89.4 (104)
Bronson	100.0 (5)	100.0 (17)	87.1 (31)	80.8 (26)	89.9 (79)
Meadow Hills	100.0 (2)	88.9 (9)	87.5 (8)	90.0 (10)	89.7 (29)
Churchill	66.7 (3)	100.0 (4)	100.0 (14)	71.4 (7)	85.7 (28)
Manitoba Lowland		100.0 (6)		100.0 (1)	100.0 (7)
PA Uplands	100.0 (2)	100.0 (3)	100.0 (4)	0 (1)	90.0 (10)
Mostoos Upland		100.0 (2)		100.0 (5)	100.0 (7)
Cub	90.0 (10)	88.9 (9)	80.0 (5)	66.7 (3)	85.2 (27)
Foster	100.0 (1)	100.0 (4)	85.7 (7)	100.0 (5)	94.1 (17)
Uranium City				71.4 (14)	71.4 (14)

* number of uteri collected from adult beaver during reproductive period in parenthesis

Appendix V Prenatal mortality of Saskatchewan beaver*

Habitat	1965	1966	1967	1968	Mean
South-Saskatchewan	0 (2)**	6.7 (3)	9.1 (6)		6.9 (11)
Pasquia	11.3 (13)	10.5 (19)	16.0 (20)	10.0 (26)	11.9 (78)
Porcupine	12.0 (27)	11.1 (24)	13.3 (27)	8.5 (16)	11.4 (94)
Bronson	18.2 (3)	14.1 (14)	9.4 (32)	8.6 (22)	10.4 (71)
Meadow Hills		21.0 (16)	2.4 (8)	5.6 (14)	11.7 (38)
Churchill	0 (1)	7.7 (9)	9.4 (13)	12.5 (2)	8.7 (25)
Manitoba Lowland		10.4 (7)		0 (1)	6.7 (8)
PA Uplands		40.0 (2)	18.2 (5)		25.0 (7)
Mostoos Upland		31.2 (4)		25.0 (4)	28.1 (8)
Cub	10.0 (9)	20.6 (10)	0 (2)	0 (2)	14.1 (23)
Foster	25.0 (2)	6.7 (4)	28.6 (4)	17.6 (5)	18.0 (15)
Uranium City				16.7 (8)	16.7 (8)

* all ages of females combined

** number of females with complete corpora lutea and fetal counts in parenthesis

Appendix VI Resorption rates of Saskatchewan beaver

Habitat	1966	1967	1968	Mean
South-Saskatchewan	0 (5)*	3.23 (6)		1.79 (11)
Pasquia	0 (29)	7.87 (26)	2.26 (29)	3.27 (84)
Porcupine	0.68 (31)	4.31 (27)	3.49 (20)	2.58 (78)
Bronson	0.80 (29)	3.51 (38)	4.10 (27)	2.87 (94)
Meadow Hills	1.30 (19)	1.82 (12)	3.77 (14)	2.16 (45)
Churchill	2.50 (10)	4.49 (25)	0 (6)	2.27 (41)
Manitoba Lowland	0 (7)		0 (1)	0 (8)
PA Uplands	0 (4)	0 (5)		0 (9)
Mostoos Upland	0 (6)		5.88 (5)	2.70 (10)
Cub	12.90 (10)	0 (4)	0 (2)	8.16 (16)
Foster	0 (4)	11.10 (7)	5.88 (6)	6.12 (17)
Uranium City			13.79 (10)	13.79 (10)

* number of beaver with fetuses in parenthesis

Appendix VII Frequency of beaver of various ages in the 1965-66 harvest in Saskatchewan (%)

Habitat	n	Age-group																	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	20
SS	18	55.6	16.7	11.1			5.6	11.1											
P	56	37.5	23.2	12.5	5.4	5.4	5.4		1.8	5.4		1.8		1.8					
Py	108	39.8	26.9	5.6	9.3	5.6	5.6	2.8	0.9	2.8					0.9				
B	212	45.3	14.6	14.2	9.9	6.1	3.3	2.8		0.9	0.9	0.5			0.5		0.5	0.5	
MH	81	22.2	35.8	18.5	4.9	4.9	4.9	2.5	2.5	1.2	1.2					1.2			
Ch	254	33.1	27.2	11.4	8.3	6.7	3.5	1.6	1.6	2.0	1.2	0.8	0.8	0.4	0.4	0.4	0.4	0.4	
ML	40	25.0	32.5	22.5	5.0	5.0		5.0	2.5										2.5
PA	72	43.1	25.0	8.3	6.9	5.6	2.8	1.4	1.4	1.4	1.4	1.4		1.4					
Mo																			
C	112	30.4	28.6	13.4	5.4	3.6	3.6	2.7	3.6	1.8	0.9	2.7		0.9		1.8	0.9		
F	22	4.5	9.1	13.6	18.2	9.1	4.5	4.5	13.6				13.6				4.5		4.5
UC																			

n=number of beaver aged: 1=½-1; 2=1½-2; etc.

Appendix VIII Frequency of beaver of various ages in the 1966-67 harvest in Saskatchewan (%)

Habitat	n	Age-group																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	20
SS	45	48.9	17.8	8.9	15.6	4.4				2.2						2.2		
P	149	65.8	14.1	6.0	4.7	2.0	2.0	1.3		2.0	0.7	1.3						
Py	336	50.9	19.0	7.1	6.9	1.5	2.7	2.1	4.2	1.5	0.6	0.6	0.9	0.6	0.6	0.6		0.3
B	426	53.1	14.8	9.2	8.2	3.3	3.3	2.3	1.6	1.2	0.9	1.4	0.2	0.5				
MH	162	56.2	11.7	12.3	8.0	1.2	1.2	2.5	3.1	1.2		1.2		0.6				0.6
Ch	109	34.9	19.3	11.0	18.3	5.5	6.4	1.8		0.9	0.9					0.9		
ML	97	58.8	8.3	13.4	3.1	5.2	1.0		2.1		1.0	1.0	2.1	1.0	1.0	2.1		
PA	90	32.2	22.2	20.0	12.2	1.1	1.1	2.2	4.4	2.2	1.1		1.1					
Mo																		
C	188	40.4	19.1	14.4	8.0	2.7	3.2	2.1	2.7	1.1	2.1	0.5	2.1	0.5		0.5	0.5	
F	91	13.2	25.3	13.2	18.7	7.7	9.9	5.5	3.3	1.1		1.1		1.1				
UC																		

n=number of beaver aged: 1=½-1; 2=1½-2; etc.

Appendix IX Frequency of beaver of various ages in the 1967-68 harvest in Saskatchewan (%)

Habitat	n	Age-group																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	19
SS																		
P	329	47.4	28.9	7.9	3.0	1.8	2.1	0.9	1.2	2.4	1.2	0.3	0.9	0.9	0.3	0.3	0.3	0.3
Py	174	47.7	29.3	5.7	2.9	1.7	0.6	0.6	3.4	2.3	2.9	2.3	0.6					
B	475	46.7	24.4	10.3	7.8	4.0	2.3	0.4	2.1	0.8	0.6				0.2	0.2		
MH	269	40.5	24.2	13.0	7.8	2.6	3.3	0.7	1.9	1.5	1.5	0.7		1.1	0.7	0.4		
Ch	204	35.8	23.5	9.3	8.8	8.8	4.4	2.4	1.5	2.0	1.0		1.0		1.0	0.5		
ML																		
PA	80	36.3	26.3	13.8	10.0	7.5	1.3	1.3		1.3	1.3				1.3			
Mo	61	63.9	16.4	1.6	4.9		1.6		6.5		4.9							
C	155	17.4	19.4	17.4	16.1	5.8	1.9	3.9	5.2	2.6	3.2	2.6	0.6		1.9	1.3	0.6	
F	116	8.6	21.6	19.0	17.2	5.2	6.0	4.3	6.0	3.4	1.7	4.3	0.9			0.9	0.9	
UC	53	28.3	5.7	13.2	9.4	17.0	13.2	11.3		1.9								

n=number of beaver aged: 1=½-1; 2=1½-2; etc.